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WHEAT Growth & Development

This book describes the growth and development of the wheat plant from germination to grain filling.

The environmental factors and management actions that influence each growth stage are also discussed.

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Wheat growth & development

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Contents

Preface

This book describes the growth and development of the wheat plant from germination to grain filling. The environmental factors and management actions that influence each growth stage are provided as a practical reference for managing crops.

Photo: L Turton

The aim of *Wheat growth and development* is to link plant physiology and crop management. It will help agronomists and farmers to understand the life cycle of the wheat plant, and the factors that influence growth and development, and to identify the growth stages of the wheat plant using Zadoks decimal growth scale. This knowledge can then be applied to crop management to maximise yield and profit.

There are four chapters in the book covering the progression of key stages in the life cycle of the wheat plant, its growth and management. Included in each chapter are practical exercises to demonstrate how knowledge of plant physiology can be applied in the paddock.

Introduction

Growing wheat

Wheat evolved from wild grasses and is thought to have first been cultivated between 15,000 and 10,000 BC. It is an annual plant belonging to the genus *Triticum* which includes common bread wheat (*Triticum aestivum)* and durum (*Triticum turgidum*).

Wheat is the largest grain crop in Australia. Australian wheat farmers produce around 16 million tonnes of wheat each year, 70% of which is exported. In world terms, Australia is the fourth largest exporter, contributing around 11% of world trade, and is the largest producer and exporter of white wheat in the world. Asia, the Middle East and the Pacific are the principal export destinations while the domestic market is the largest single market and is growing rapidly.

Figure i: Wheat growing areas in Australia.
Source: NSW DPI.

New South Wales production

Wheat is the main crop grown in New South Wales, which is the second-highest producing State in Australia. Around 7.9 million tonnes of grain was produced in New South Wales in 2005–2006.

Wheat can be grown in almost all areas of the state where cropping is possible (Figure i). The level of production is sensitive to seasonal conditions and the price of wheat. The average area planted to wheat during the 1990s in New South Wales was 2.4 million hectares with an average yield of 2.0 t/ha (Figure ii).

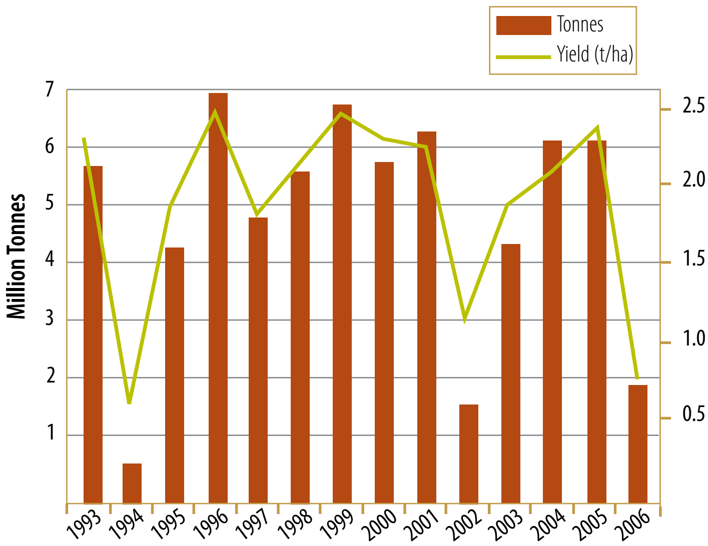


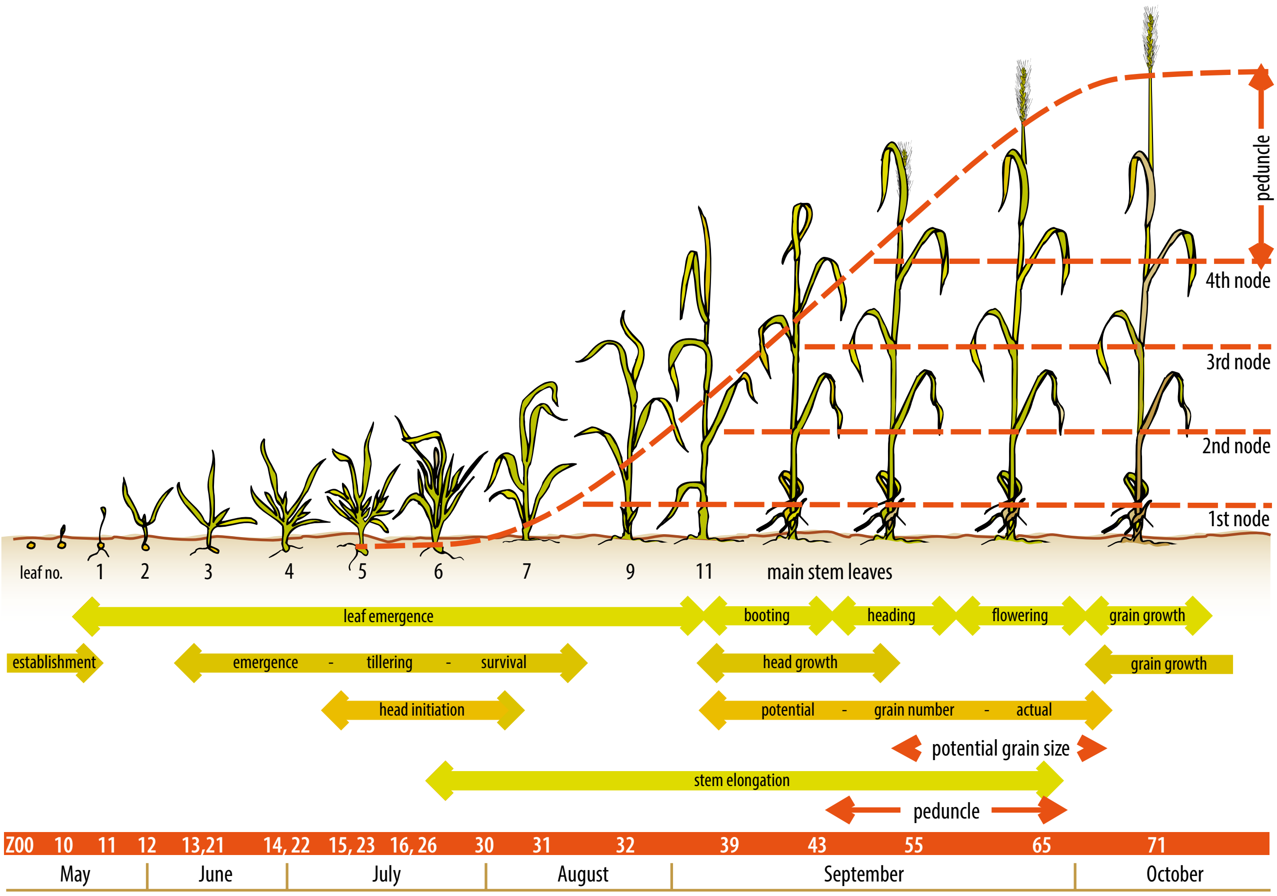
Figure ii: NSW wheat production for 1993–2006.
Source: F Scott, 2006.

Wheat types

Winter and spring wheats are the two types of wheats grown in New South Wales. The main difference between the two types is that winter wheats need a period of cold temperatures to begin reproduction while spring wheats do not have a cold requirement.

Winter wheats

Winter wheats are commonly used in the mixed farming zones. Winter wheats need to experience a certain period of cold temperatures, between 0° and 10°C, to trigger a switch from vegetative growth to flowering (anthesis). This cold requirement is known as vernalisation. The winter wheat varieties need different periods of vernalisation, so it is important to take this into consideration when selecting a variety. The vernalisation requirement means that winter wheats adapt to varying sowing times and so can be used for the dual purpose of grazing and grain. They can be sown from February to early April for grazing, depending on the vernalisation requirement of the variety.



* under good condition some plants will have a coleoptile tiller appearing between Z11 and Z12

Figure iii: Life cycle of the wheat plant.
Source: Based on M Stapper, 2007.

Spring wheats

The vast majority of wheat varieties grown in New South Wales are spring wheats. Spring wheats grow and develop in response to increasing temperature and photoperiod (daily hours of light). They do not have a vernalisation requirement to initiate flowering and so are grown in the warmer regions of New South Wales. It is very important to sow spring wheats at the recommended time to minimise the risk of frost damage during flowering. Recommended sowing times are published each year by the NSW Department of Primary Industries in the *Winter crop variety sowing guide.*

Life cycle

The growth and development of the wheat plant is a complex process. During the life cycle of the plant, many of the growth stages overlap, and while one part of the plant may be developing another part may be dying. Figure iii represents the progression of the key growth stages, where they overlap, and the point where potential and actual yield are set. Zadoks references are also shown, and the main plant parts are identified.

Zadoks decimal growth scale

Effective crop management depends on being able to identify the growth stage of the crop. This is where a growth scale becomes a valuable tool.

A growth scale provides a common reference for describing a growth stage that enables better communication between farmers, agronomists, researchers and other agricultural professionals. An example of where this is important is in the timing of fertiliser and chemical applications.

A number of growth scales are in use around the world, with the Feekes, Zadoks and Haun scales the most widely applied. Growth stages are denoted in a number of ways, including GS (growth stage) and DC (decimal code). In this book, the Zadoks growth scale is used, indicated by Z (Table i).

Table i: Zadoks decimal growth scale for cereals.

GERMINATION	
00	Dry seed
01	Start of imbibition
03	Imbibition complete
05	Radicle emerged from seed
07	Coleoptile emerged
09	Leaf just at coleoptile tip
SEEDLING GROWTH	
10	First leaf through coleoptile
11	First leaf unfolded
12	2 leaves unfolded
14	4 leaves unfolded
16	6 leaves unfolded
18	8 leaves unfolded
TILLERING	
20	Main shoot only
21	Main shoot & 1 tiller
22	Main shoot & 2 tillers
24	Main shoot & 4 tillers
26	Main shoot & 6 tillers
28	Main shoot & 8 tillers
STEM ELONGATION	
30	Stem starts to elongate, "*head at 1 cm*"
31	1st node detectable
32	2nd node detectable
34	4th node detectable
36	6th node detectable
37	Flag leaf just visible
39	Flag leaf/collar just visible
BOOTING	
41	Flag leaf sheath extending
43	Boot just visibly swollen
45	Boot swollen
47	Flag leaf sheath opening
49	First awns visible
HEAD EMERGENCE	
50	1st spikelet of head just visible
53	1/4 of head emerged
55	1/2 of head emerged
57	3/4 of head emerged
59	Emergence of head complete
ANTHESIS (FLOWERING)	
61	Beginning of anthesis
65	Anthesis 50%
69	Anthesis compete
MILK DEVELOPMENT	
71	Seed watery ripe
73	Early milk
75	Medium milk
77	Late milk
DOUGH DEVELOPMENT	
83	Early dough
85	Soft dough
87	Hard dough
RIPENING	
91	Seed hard (difficult to divide by thumbnail)
92	Seed hard (can no longer be dented by thumbnail)
93	Seed loosening in daytime
94	Overripe, straw dead & collapsing
95	Seed dormant
96	Viable seed giving 50% germination
97	Seed not dormant
98	Seed dormancy induced

Source: Based on J Zadoks, T Chang & C Konzak, 1974.

Zadoks is a decimal growth scale proposed for cereal plants by J Zadok, T Chang and C Konzak in 1974. The scale is based on 10 primary growth stages (0–9). Each primary growth stage is divided into 10 secondary growth stages that indicate the number of plant parts on the main stem or secondary stage of development, extending the scale from 00–99. So each point on the scale has two digits, the first indicating the growth stage and the second the number of plant parts or secondary stages of development. For example, Z15 means growth stage 1 with 5 leaves on the main stem. Z24 means growth stage 2 with 4 tillers. Several of the growth stages occur together, so a plant may have more than one decimal code applied at the same time. For example, a plant may be producing leaves and tillering at the same time and so could have a code of Z15, 22, meaning it has 5 leaves on the main stem and 2 tillers.

Where appropriate, throughout *Wheat growth and development* a Zadoks reference is provided for the development stage under discussion. Zadoks decimal growth scale is provided in Table i.

The wheat grain

The wheat grain is the reproductive unit of the wheat plant as well as the end-use product. A wheat grain can be broadly divided into three components (Figure iv):

- seed coat and aleurone layer (or bran)
- endosperm
- embryo (germ).

In most varieties, the proportion of each component of the grain is 14% seed coat, 83% endosperm and 3% embryo.

Seed coat: the outer protective covering of the seed.

Aleurone: a layer of protein surrounding the endosperm that secretes enzymes to break down starch reserves in the endosperm.

Endosperm: Tissue that surrounds the embryo and provides energy for germination. The germinating seed relies on these reserves until it has developed a root system. It makes up the bulk of the grain and stores the starch and protein that are milled for the production of white flour.

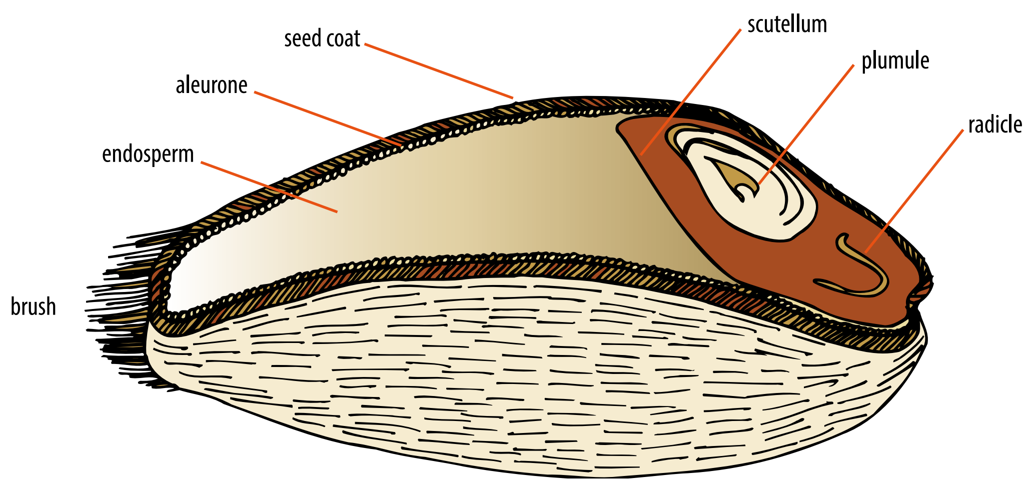


Figure iv: The wheat grain.
Source: wheatbp.net.

Embyro: contains the main plant structures, so it holds all the elements of the growing plant. It is made up of the scutellum, plumule (shoot) and radicle (primary root). It is found at the point where the grain is attached to the spikelet.

- *Scutellum:* a shield–shaped structure that absorbs the soluble sugars from the breakdown of starch in the endosperm. It also secretes some of the enzymes involved in germination.
- *Plumule:* the growing point of the seed that develops into the shoot bearing the first true leaves. At the growing point is the coleoptile, three leaf primordia and the shoot apex.
- *Radicle:* develops into the primary root and is the first structure to emerge after germination.

Once filled, the wheat grain is 70% carbohydrate, and 97% of this carbohydrate is starch (Figure v). The protein content is between 8% and 15%, depending on final grain weight; this equates to between 4 and 10 mg.

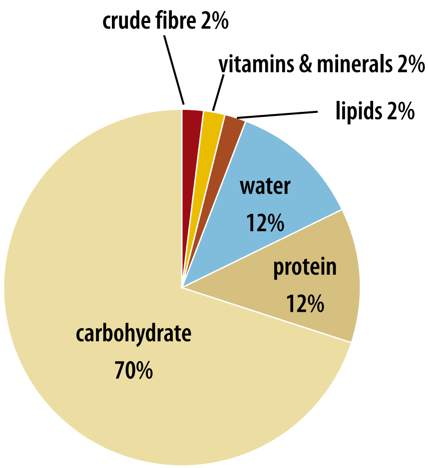


Figure v: The basic ingredients of the wheat grain.
Source: Based on P Stone & M Nicolas, 1996.

The wheat plant

The main structures of the plant are the coleoptile, leaves, tillers, stem, roots and head.

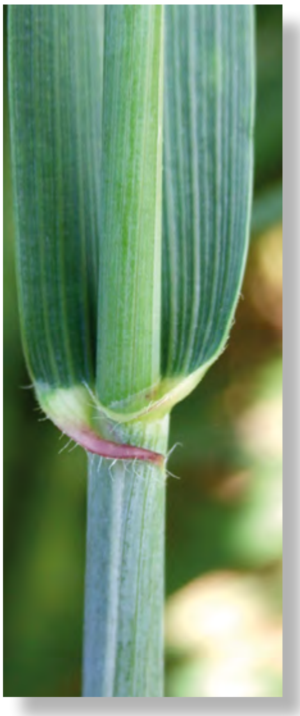
Coleoptile

The coleoptile is a protective sheath that encases the first leaf. It pushes through the soil to the surface.

Leaves

The leaf consists of a sheath, which wraps around the newly emerging leaf, and a leaf blade. The leaf sheath contributes to stem strength. The leaf collar is the point where the leaf sheath joins the leaf blade. The leaf collar has two features, the ligule and the auricles. The ligule is a thin colourless membrane around the base of the collar. The auricles are small hairy projections that extend from the side of the leaf collar. These features can be used to help identify grass species (Figure vi).

Leaves are produced in a set order, on alternate sides of the stem. The final leaf to grow before head emergence is the flag leaf.



Leaf collar showing the ligule and auricles.
Photo: J White.

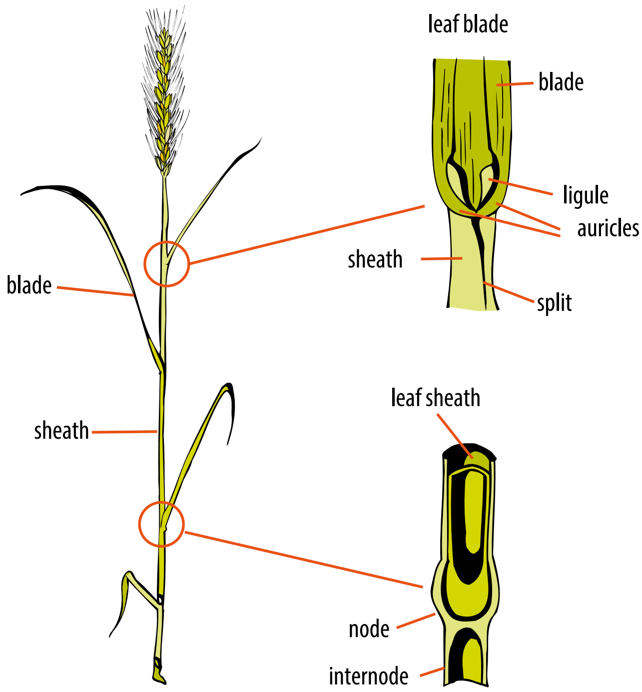


Figure vi: Structure of the leaf.
Source: Based on W Anderson & J Garlinge, 2000.

Tillers

Tillers are lateral branches or shoots that arise from buds in the axil of the leaves at the base of the main stem. Primary tillers are produced from the leaves of the main stem and can form their own, secondary tillers.

Stem

The stem is made up of nodes and internodes. Nodes are where structures such as leaves, roots, tillers and spikelets join the stem. The internode is the tissue between adjacent nodes that elongates as the stem grows. The stem is wrapped in the sheaths of the surrounding leaves.

This structure of stem and leaves gives strength to the shoot, helping to keep the plant upright.

As the stem grows it changes function from providing support for leaves to storing carbohydrates and nutrients for grain filling.

Roots

Wheat has primary and secondary root systems (Figure vii). The first roots to appear are the primary roots (also called seminal or seedling roots). At germination, the radicle breaks through the seed coat, followed by four or five lateral roots. These form the primary root system that supports the plant until the secondary root system develops. The secondary roots (also called adventious, nodal or crown roots) initiate from nodes within the crown after germination.

Roots of a wheat plant
Photo: L Turton.

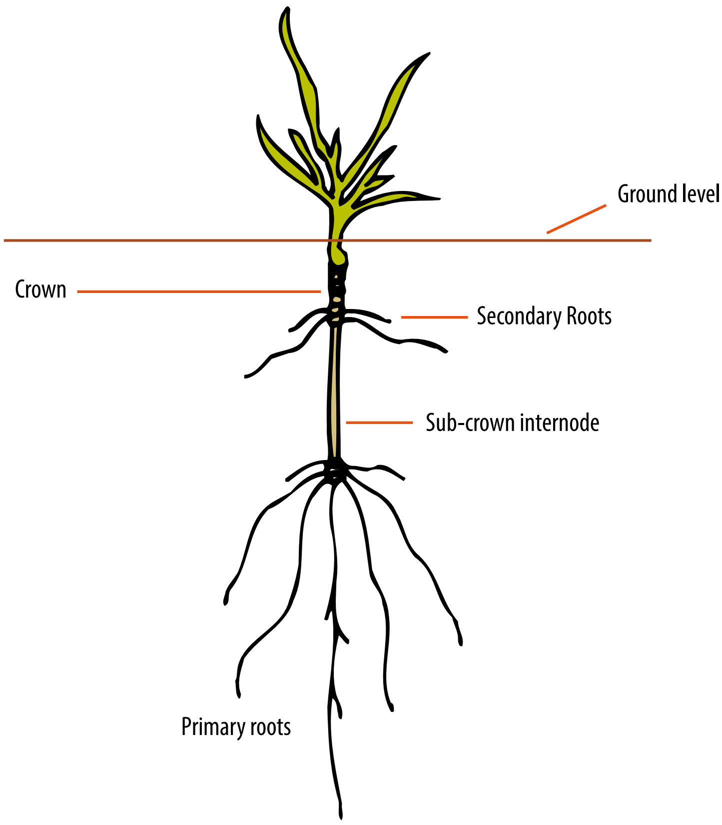


Figure vii: The wheat plant, showing the primary and secondary root systems.
Source: Based on W Anderson & J Garlinge, 2000.

Head

The head of the wheat plant has a rachis (stem) made up of nodes and short, flattened internodes. At the nodes are the floral structures, called spikelets, that hold up to 10 florets containing the flower of the wheat plant, where grain is formed. Figure viii shows the structure of the wheat head, spikelet and floret.

Each floret is enclosed within two protective bracts called the lemma and palea. These structures wrap around the carpel. The carpel contains the ovary with the feathery stigmas, three stamens holding the anthers (pollen sacs), and the ovule. Once fertilised, the ovule forms the grain.

Figure ix shows the structure of the floret, and the location of florets on the spikelet.

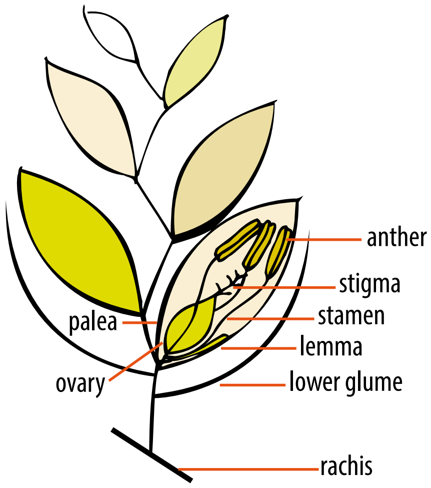


Figure ix: A spikelet showing the structures of the floret.
Source: Based on E Kirby & M Appleyard , 1984.

Wheat head.
Photo: M Dignand.

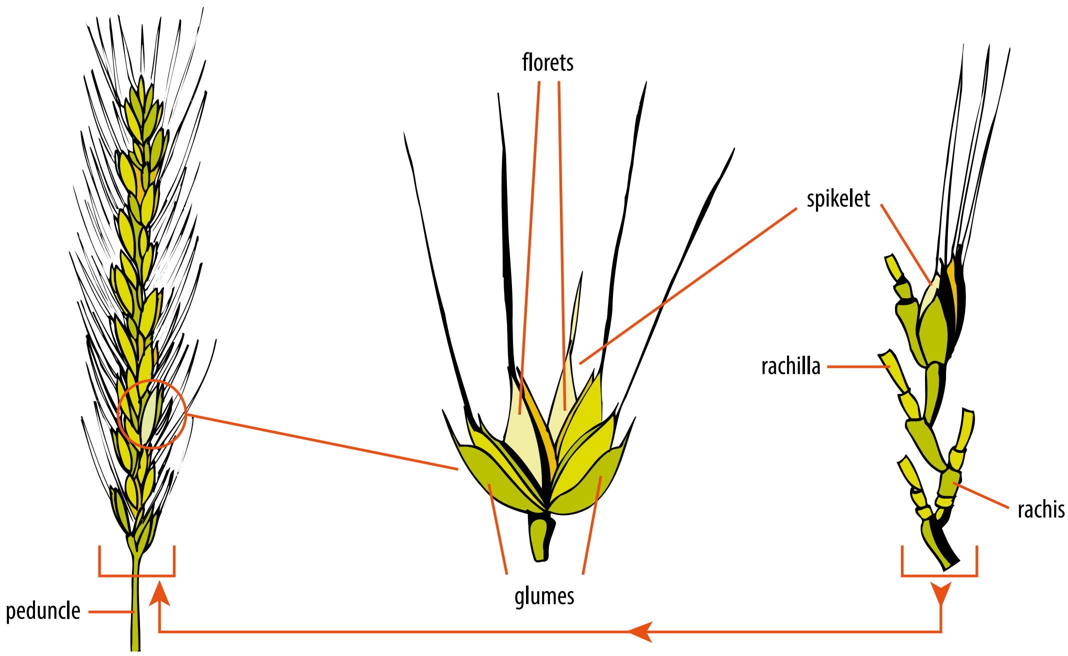


Figure viii: Structures of the head, showing the spikelet and floret.
Source: Based on W Anderson & J Garlinge, 2000.

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1. Germination & emergence

by Phillip Bowden & Nathan Ferguson

Chapter Snapshot

Introduction

Under the right conditions, a viable wheat seed germinates. Chapter 1 is about the processes that see the first shoot emerge from the ground and the beginning of root growth. The phases covered in this chapter are germination, emergence and establishment.

Learning Outcomes

At the end of this chapter, you will be able to:

- describe the germination process and the role of moisture, temperature and oxygen
- explain plant emergence and establishment and the role of moisture and temperature
- understand the factors that influence coleoptile length
- recognise the qualities to look for when selecting seed
- conduct a germination and 1000-grain weight test
- calculate a sowing rate to target a plant population.

Radicle
part of the seed embryo that grows into the primary root.

Germination–Z00

Germination begins when the seed absorbs water and ends with the appearance of the radicle. Germination has three phases:

- water absorption (imbibition)
- activation
- visible germination (see Figure 1–1).

Phase 1 Water absorption (Z01)

Phase 1 starts when the seed begins to absorb moisture. As a general rule, a wheat seed needs to reach a moisture content of around 35% to 45% of its dry weight to begin germination. Water vapour can begin the germination process as rapidly as liquid can. Wheat seeds begin to germinate at a relative humidity of 97.7%. Soil so dry that roots can't extract water still has a relative humidity of 99%, much higher than that of a dry seed. So even in dry conditions, there can be enough moisture for the seed to absorb and begin Phase 1, but it takes longer.

Phase 2 Activation (Z03)

Once the embryo has swollen it produces hormones that stimulate enzyme activity. The enzymes break down starch and protein stored in the seed to sugars and amino acids, providing energy to the growing embryo. If the seed dries out before the embryo starts to grow it remains viable.

Phase 2 continues until the rupture of the seed coat, the first visible sign of germination.

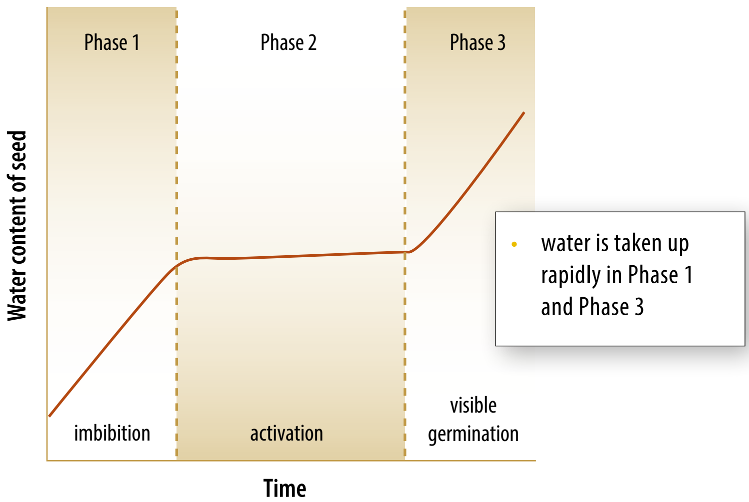


Figure 1–1: Pattern of water uptake by wheat seeds in a moist environment.
Source: Based on J. Passioura, 2005.

Phase 3 Visible germination (Z05–Z09)

In Phase 3 the embryo starts to visibly grow. The radicle emerges followed soon after by other primary roots and the coleoptile. The enzymes produced in Phase 2 mobilise sugars and amino acids stored in the seed and enable their transfer to the growing embryo.

Emergence–Z07

As the first primary roots appear the coleoptile bursts through the seed coat and begins pushing towards the surface. Emergence is when the coleoptile or the first leaf becomes visible above the soil surface. (See *Chapter 2: Vegetative growth* for detail on root growth).

Coleoptile formation

The coleoptile is well developed in the embryo, forming a thimble-shaped structure covering the seedling tube leaf and the shoot. Once the coleoptile emerges from the seed it increases in length until it breaks through the soil surface.

The fully elongated coleoptile is a tubular structure about 50 mm long and 2 mm in diameter. It is white, except for two strands of tissue that contain chlorophyll. The end of the coleoptile is bullet shaped and is closed except for a small pore, 0.25 mm long, a short distance behind the tip.

When the coleoptile senses light it stops growing and the first true leaf pushes through the pore at the tip. Up to this point the plant is living on reserves within the seed.

Establishment–Z10

The plant is established once it has roots and a shoot. It is no longer relying on reserves in the seed as it is producing its own energy.

Factors affecting germination and emergence

Dormancy

In a wheat seed, germination begins after a very short period of dormancy. Australian wheats have a low level of dormancy that it is easily broken down, allowing germination to begin. By contrast, European and North American red wheat varieties have a dormancy derived from their seed coat that lasts 3 to 7 months. This dormancy is linked to the enzymes called anthocyanins that give the seed coat the red colour.

In Australian white wheats at least two genes influence the level of dormancy. One gene is in the embryo of the seed and needs to be present for any level of seed dormancy to develop. This gene makes the grain sensitive to the plant hormone abscisic acid, which prevents germination at the time of crop maturity.

The second gene is in the seed coat and, in combination with the embryo gene, produces a more robust and stable dormancy. This level of dormancy is essential in varieties targeted for Queensland and northern New South Wales because of summer rainfall, and is highly desirable in southern Australia. (See also *Chapter 4: Grain development, Pre-harvest sprouting*).

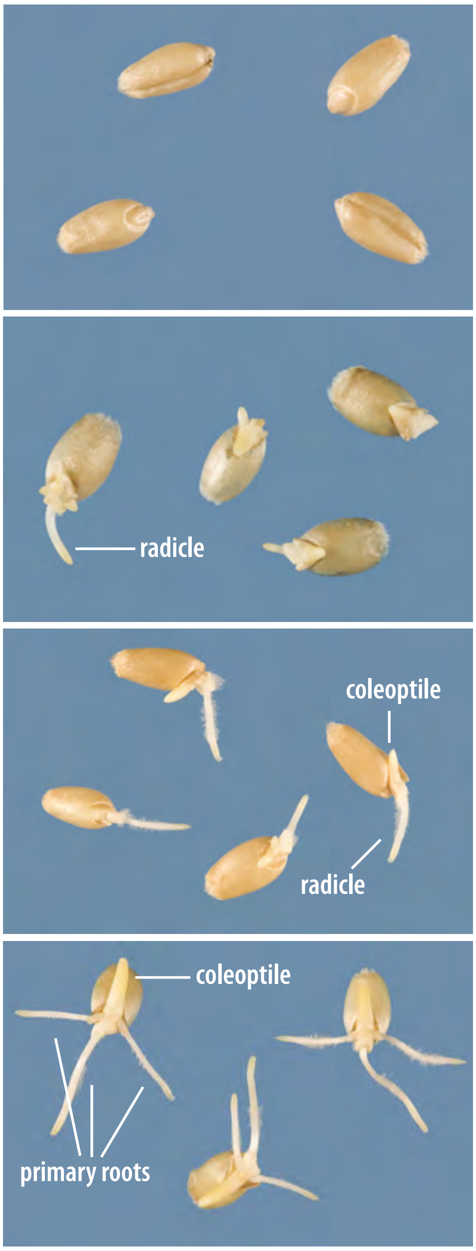


Figure 1–2: Germinating wheat seeds with the radicle and coleoptile emerging. Photo: L Turton.

Moisture

Soil moisture influences the speed of germination. Germination is rapid if the soil is moist. When the soil dries to near the permanent wilting point, the speed of germination slows. Instead of 5 days at 7°C when there is adequate moisture, germination will take 10 days at 7°C when soil reaches the permanent wilting point.

The germination process in a seed may stop and start in response to available moisture. So seeds that have taken up water and entered Phase 2, but not reached Phase 3, remain viable if the soil dries out. This can happen when dry sowing is followed by a small fall of rain that keeps the soil moist for a few days

Permanent wilting point (or crop lower limit) is the point at which roots can't extract water.

before drying out. When the next fall of rain comes, the seed resumes germinating, taking up water and moving quickly through Phase 2 so that germination is rapid.

This ability to start and stop the germination process (in response to conditions) before the roots and coleoptile have emerged is an important consideration when dry sowing. If the seed bed dries out before the coleoptile has emerged, the crop needs to be monitored to determine if it will emerge so that the critical decision to re-sow can be made.

Soil moisture also affects emergence. Sowing into hard setting or crusting soils that dry out after sowing may result in poor emergence. The hard soil makes it difficult for the coleoptile to push through to the surface, particularly in varieties with short coleoptiles.

In some crusting soils, gypsum and/or lime may improve soil structure and assist seedling emergence.

Stubble reduces the impact of raindrops on the soil surface and helps prevent soil crusts from forming. Stubble retention also encourages biological activity and increases the amount of organic matter, which improves the stability of the soil by binding the soil particles together.

Temperature

Germination

Germination is dependent on temperature. The ideal temperature for wheat germination is between 12° and 25°C, but germination will occur between 4° and 37°C.

The speed of germination is driven by accumulated temperature or degree–days. Degree-days are the sum of the average daily maximum and minimum temperatures over consecutive days. Wheat requires 35 degree-days for visible germination to occur (see Table 1–1). For example, at an average temperature of 7°C

Table 1–1: Degree-days required for germination and emergence.

NO. OF DEGREE-DAYS REQUIRED	
Root just visible	27
Coleoptile visible	35
Emergence (40 mm)	130
Each leaf	100

Source: J Passioura, 2005.

Table 1–2: Examples of how different temperatures affect germination.

TEMPERATURE	NO. OF DAYS TO GERMINATION
3.5°C	10
5°C	7
7°C	5
10°C	3.5

Source: J Passioura, 2005.

it takes 5 days before visible germination. At 10°C it takes 3.5 days. Other examples are presented in Table 1–2. (See also *Chapter 2: Vegetative growth, Thermal time).*

Emergence

Extension of the coleoptile is directly related to soil temperature. Soils that are too cold or too hot shorten the coleoptile length. Research shows that coleoptiles are longest when soil temperatures are between 10° and 15°C. This is one reason why there is variation in emergence and establishment in the different wheat-growing areas.

Establishment

Plant emergence and establishment are the starting points of crop growth. High temperatures during establishment cause seedling mortality, reducing the number of plants that establish. In hot environments, the maximum temperature in the top few centimetres of soil can be 10° to 15°C higher than the maximum air temperature, especially with a dry, bare soil surface and high radiation intensity. In these conditions, soil temperature can reach 40° to 45°C, seriously affecting seedling emergence. Brief exposure to extreme soil temperatures can also restrict root growth and tiller initiation.

Table 1–3 shows the average number of plants that established with increasing soil temperatures. The equivalent to 100 kg seed/ha was planted at a depth of 30 to 40 mm. The soil temperature was measured in the field at a depth of 50 mm.

Table 1–3: Number of wheat plants established at various soil temperatures.

MEAN MAX SOIL TEMP (°C)	PLANTS ESTABLISHED (plants/m^2)
20.2°C	315.3
33.2°C	256.7
42.2°C	89.8

Note: the difference between 20.2°C and 33.2°C is statistically significant.

Source: E Acevedo, P Silva & H Silva, 2002.

Oxygen

Oxygen is essential to the germination process. Seeds absorb oxygen rapidly during germination, and without enough oxygen they die. Germination is slowed when the soil oxygen concentration is below 20%. During germination, water softens the seed coat to make it permeable to oxygen, so dry seeds absorb almost no oxygen.

Seeds planted in waterlogged soils can't germinate, because of a lack of oxygen. It is commonly thought that in very wet conditions seeds 'burst', but they run out of oxygen and die.

Seed quality

Early seedling growth relies on stored energy reserves in the seed. Good seedling establishment is more likely if seed is undamaged, stored correctly and from a plant that had adequate nutrition. Seed grading is an effective way to separate good quality seed of uniform size from small or damaged seeds and other impurities.

Seed size is also important—the larger the seed, the larger the endosperm and starch reserves. So while size does not alter germination, bigger seeds have faster seedling growth, a higher number of fertile tillers per plant and potentially higher grain yield.

Seed size is usually measured by weighing 1000 grains, known as the 1000-grain weight. Table 1–4 and Table 1–5 show the long term 1000-grain weight averages for several wheat varieties, and survey data from seed harvested in 2002, 2003 and 2006. The results show that 1000-grain weights vary among varieties and from season to season. This indicates that sowing rate needs to vary according to the 1000-grain weight for each variety, in each season, in order to achieve desired plant densities.

Table 1–4: Comparison of long term average 1000-grain weight with the averages from farmer samples for southern New South Wales.

	1000-GRAIN WEIGHT		FARMER SAMPLES
VARIETY	SE NSW 1999–2005	SW NSW 1999–2005	N NSW 2006
EGA_Gregory	36.0	38.5	28.5 (8)
Ellison	41.9	42.5	33.6 (25)
Sunstate	36.8	–	30.5 (14)
Ventura	39.6	38.7	33.6 (64)

Figures in parenthese are the number of farmer samples.

Source: *Winter crop variety sowing guide* and G McMullen 2007, 'Seed survey', District Agronomist Update, Parkes.

Table 1–5: Comparison of long term average 1000–grain weight with the averages from farmer samples for northern New South Wales.

	1000-GRAIN WEIGHT		FARMER SAMPLES	
VARIETY	NE NSW 1999–2005,	NW NSW 1999–2005,	N NSW 2002	N NSW 2003
H45	35.0	33.4	36.8 (8)	33.1 (10)
Kennedy	38.0	36.3	41.3 (9)	33.2 (8)
Strzelecki	37.3	35.4	37.7 (9)	33.7 (14)
Sunstate	37.1	35.4	38.8 (9)	31.2 (10)
Sunvale	33.8	31.6	34.4 (12)	27.9 (8)

Figures in parenthese are the number of farmer samples.

Source: *Winter crop variety sowing guide* and J Edwards 2003, 'Plant population report', NSW Department of Primary Industries.

Weather-damaged seed is more likely to have reduced germination and emergence (Table 1–6). Further reduction may be caused by stress from azole seed dressings (a group of fungicides containing the chemical called azole), deep sowing and low soil moisture. (See also *Seed treatments* on page 16).

Coleoptile length

The length of the coleoptile is determined more by genetics than seed size or protein. Most modern semi-dwarf wheats have a dwarfing gene (Rht1 or Rht2) that reduces plant height, increases resistance to lodging and increases the ratio of grain weight to above ground dry matter (harvest index). However, these genes also produce short, weak coleoptiles usually less than 70 mm long, and poorer seedling vigour. Figure 1–3 is a comparison of the average coleoptile lengths in varieties with the Rht2 dwarfing gene, Rht8 alternative dwarfing gene, and the non-dwarfing gene, Rht.

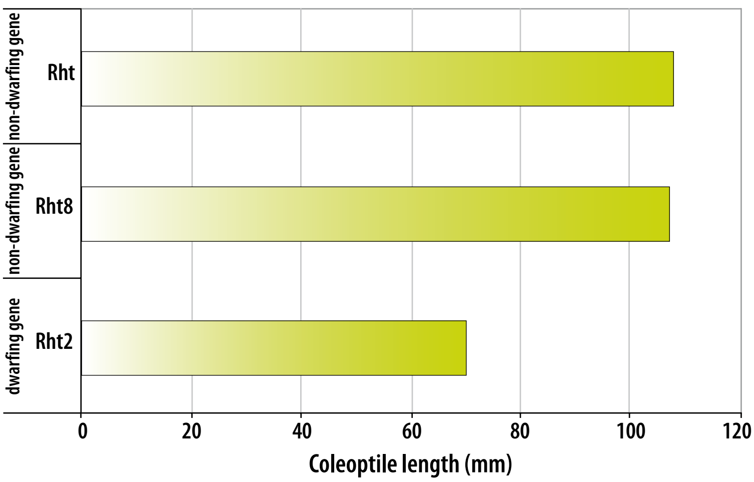


Figure 1–3: Average coleoptile length in semi–dwarf varieties, depending on dwarfing gene. Source: Based on T Botwright et al., 2001.

- Rht (non-dwarfing gene) and Rht8 (the alternative dwarfing gene) have long coleoptiles, about 100 mm.
- The Rht2 (dwarfing gene) has a much shorter coleoptile.

Table 1–6: Germination percentages of sound and weather damaged seed.

	GERMINATION (%)	
CULTIVAR	SOUND SEED	WEATHER DAMAGED SEED
Banks	83	82
Harrier *	95	85
Kite	86	88
Olympic *	92	82
Osprey *	94	84
Quarrion *	96	85
Songlen *	83	80
Sunstar *	86	70

**= indicates statistical significance.*

Source: G Murray & J Kuiper, 1988.

Varieties with shorter coleoptiles are less likely to emerge if sown too deeply, because the coleoptile is not long enough to break through to the surface. Fewer seedling plants emerge (Figure 1–4), reducing tiller numbers.

Examples of semi-dwarf varieties with a relatively long coleoptiles are Janz, Cunningham, Sunco and Lang. Varieties with short coleoptiles include Leichardt, Kennedy and Sunstate. Table 1–7 shows the coleoptile lengths of different varieties. As there is no screening data available for New South Wales, the lengths shown are based on Victorian data.

Table 1–7: Coleoptile lengths in wheat varieties.

VARIETY	COLEOPTILE LENGTH
Baxter	Medium
Chara	Medium to short
Diamondbird	Short
H45	Medium to short
Janz	Medium
Rosella	Medium to long
Sapphire	Medium
McKellar	Medium
Tennant	Medium

Source: *Victorian winter crop summary*, 2005.

Nutrition

Adequate nutrition is essential for good plant growth and development, yield and grain quality. Carry out a soil test before sowing to measure soil nutrients and calculate fertiliser requirements.

Nitrogen

Nitrogen is essential to plant growth and is commonly applied in moderate to high levels during seedbed preparation, in which anhydrous ammonia or urea is commonly used. Different forms of fertiliser nitrogen need specific management. For example, the soil needs to be moist when anhydrous ammonia is applied so it's sealed within the soil. Nitrogen can be leached from light soil if sowing is delayed by heavy rains or continuous wet weather.

Excessive nitrogen fertiliser applied close to the seed can lead to toxicity problems. Under good moisture conditions seed can tolerate a maximum of around 25 kg of nitrogen/ha without seedling mortality. This amount is based on an 18 cm row spacing. Many crops are now sown with wider row spacing. In this case, the maximum nitrogen rate needs to be lower, as the fertiliser becomes concentrated within each furrow.

Deep banding is one method of applying nitrogen fertiliser at sowing without causing seedling losses. This requires seeding systems that can separate seed and fertiliser.

Pre-drilling nitrogen is another option and can work well in minimum till or conventional systems where, for example, urea is pre-drilled with the last cultivation before sowing.

Alternatively, nitrogen fertiliser can be broadcast and incorporated at sowing, provided uniform incorporation can be achieved.

In regions of New South Wales with reliable growing season rainfall or access to irrigation, crops are usually topdressed with nitrogen.

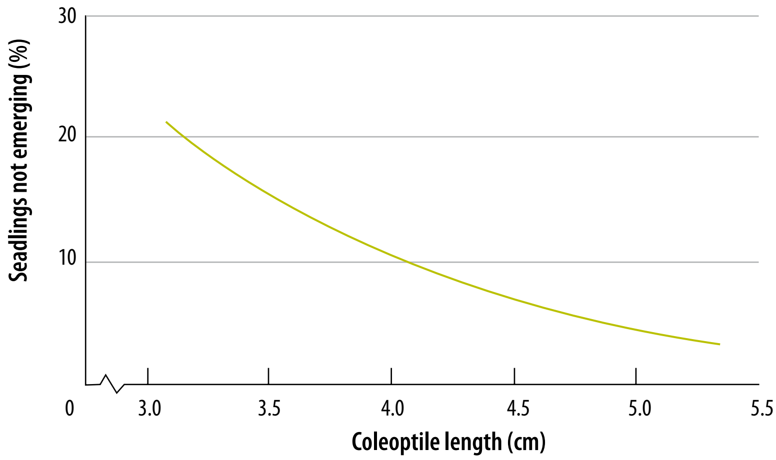


Figure 1–4: Relationship between coleoptile length and percentage of seedlings that germinated but failed to emerge.
Source: Based on P Cornish, 1986.

- The percentage of seedlings that germinate but do not emerge is greater with shorter coleoptiles.

Phosphorus

Phosphorus is essential to seed germination and early root development. Large amounts are taken up during germination. Any phosphorus deficiency at this early stage of growth significantly reduces yield potential.

Many of the soils in New South Wales have very low levels of phosphorus, and in some areas it is the limiting nutrient. Unlike nitrogen, phosphorus is relatively immobile in the soil so needs to be placed near the seed. So regardless of soil test results, some phosphorus needs to be applied at sowing in close proximity to the seed, preferably just below.

One method of estimating phosphorus requirement is to allow 4 kg phosphorus/tonne of target yield. For example, a 3 t/ha wheat crop requires 12 kg phosphorus/ha. Trials by NSW Department of Primary Industries, and grower experience, have shown that phosphorus is almost always economical to use at even higher rates.

Seed treatments

Seed treatments are applied to seed to control diseases such as smuts, bunts or rust, and insects. When applying seed treatments always read the chemical label and calibrate the applicator. Seed treatments are best used in conjunction with other disease management options such as crop and paddock rotation, clean seed, and resistant varieties.

There are some risks associated with using seed treatments. Research shows that seed treatments can delay emergence by:

- slowing the rate of germination (Figure 1–5)
- shortening the length of the coleoptile, the first leaf and the subcrown internode.

If there is a delay in emergence it increases exposure to pre-emergent attack by pests and pathogens or to soil crusting; this may lead to a failure to emerge. The risk of emergence failure is increased when seed is sown too deeply or into a poor seed bed, especially in varieties with shorter coleoptiles (see Figure 1–4).

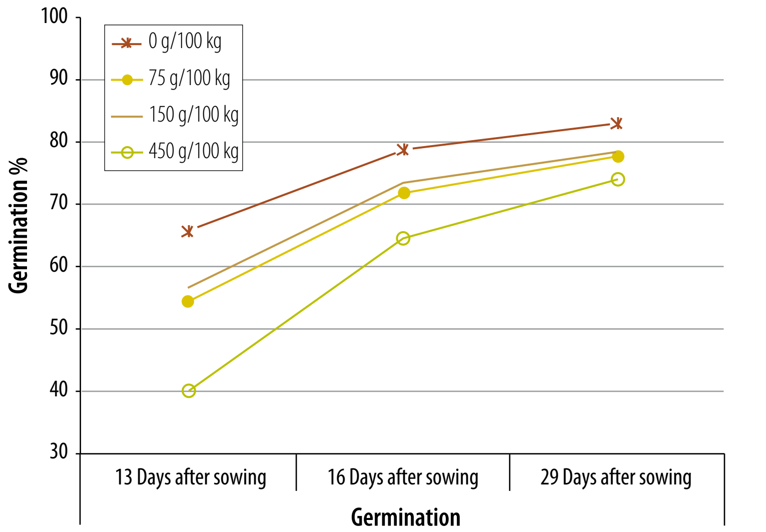


Figure 1–5: Impact of fungicide on the rate of germination.
Source: Based on P Cornish,1986.

- As the amount of certain fungicides increases, the rate of germination slows.

Some seed treatments contain azole fungicides (triadimenol and triadimefon). Research has found that these seed treatments can reduce coleoptile length, and that the reduction increases as rate of application increases (see Figure 1–6).

Sowing

Seedbed

Wheat seed needs good soil contact for germination. This can be assisted with press wheels, coil packers or rollers. Soil type determines the implement that produces the ideal seedbed.

Between 70% and 90% of seed sown produce a plant. Depth of sowing, disease, crusting, moisture and other stress in the seedbed all reduce the number of plants establishing. Field establishment is unlikely to be more than 90% and may be as low as 60% if seedbed conditions are unfavourable.

Seedbed preparation is also important to emergence. A cloddy seedbed may reduce emergence, as the clods allow light to penetrate below the soil surface. The coleoptile senses the light and stops growing while still below the surface.

Depth

Sowing depth is the key management factor for uniform rapid germination, emergence and establishment. The ideal depth to sow wheat is generally from 20 to 30 mm, depending on the availability of moisture and the variety. Depth is particularly important in varieties with short coleoptiles. In stubble trials, it was found that long coleoptile wheats emerged 30% faster than short coleoptile wheats under 6 t/ha of stubble.

Sowing depth influences the rate of emergence and the percentage that emerges, as represented in Figure 1–7. Deeper seed placement slows emergence; this is equivalent to sowing later. Seedlings emerging from greater depth are also weaker and tiller poorly.

Crop emergence is reduced with deeper sowing because the coleoptile may stop growing before it reaches the soil surface, the first leaf emerging from the coleoptile while it is still below the soil surface. As it is not adapted to pushing through soil, the leaf usually buckles and crumples, failing to emerge and eventually dying.

Photo: J Edwards.

- Higher rates of certain fungicides reduce the length of the coleoptile.

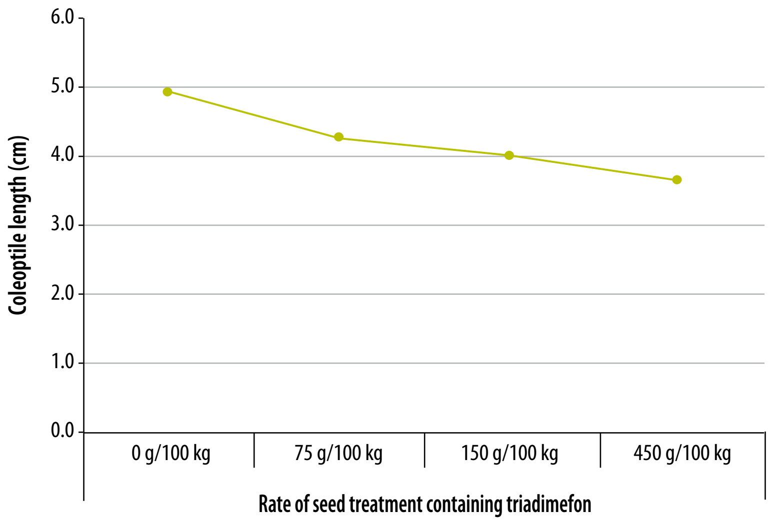


Figure 1–6: Impact of the rate of fungicide on coleoptile length.
Source: Based on P Cornish, 1986.

- Crop emergence is fastest and has the highest emergence percentage at 30–35 mm.
- At shallow depths, the soil is susceptible to evaporation and drying out, so emergence was lower at 10–15 mm sowing depth than at 30–35 mm.
- Very deep sowing (105–110 mm) slows emergence and significantly reduces the percentage emerging.

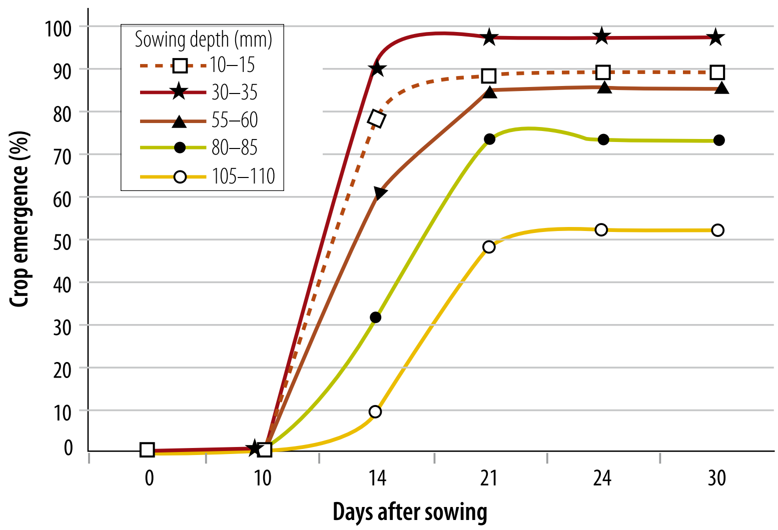


Figure 1–7: The impact of sowing depth on crop emergence.
Source: Based on J Desbiolles, 2006.

Plant population

Plant population, determined by seeding rate and establishment percentage, can be an important determinant of tiller density and, at a later stage, head density. Current recommendations for New South Wales (see *Winter crop variety sowing guide*) range from 30 to 70 plants/m^2 for the North West Plains to 100 to 150 plants/m^2 for the higher rainfall South.

High yields are possible from a wide range of plant populations, because wheat compensates by changing the number of tillers and the size of the heads in response to the environmental conditions. Despite this ability to compensate, targeting a variety's optimum plant density at sowing makes the most efficient use of water and nutrients. To reach a target plant population for the environment and seasonal conditions, adjust sowing rates to allow for:

- sowing date—higher rates with later sowings
- seed germination percentage
- seed size
- seedbed conditions
- tillage e.g. no-till
- double cropping
- soil fertility
- soil type
- field losses.

The response of different varieties to plant densities was monitored in 2003 at trial sites at Dubbo and Condobolin. Three varieties were measured at Dubbo and four at Condobolin, and at these sites densities were close to what was targeted.

At Dubbo the trial looked at the impact of plant density on:

- grain yield
- head density
- grain number per head
- mean grain weight.

The results of the trial are presented in Figure 1–8.

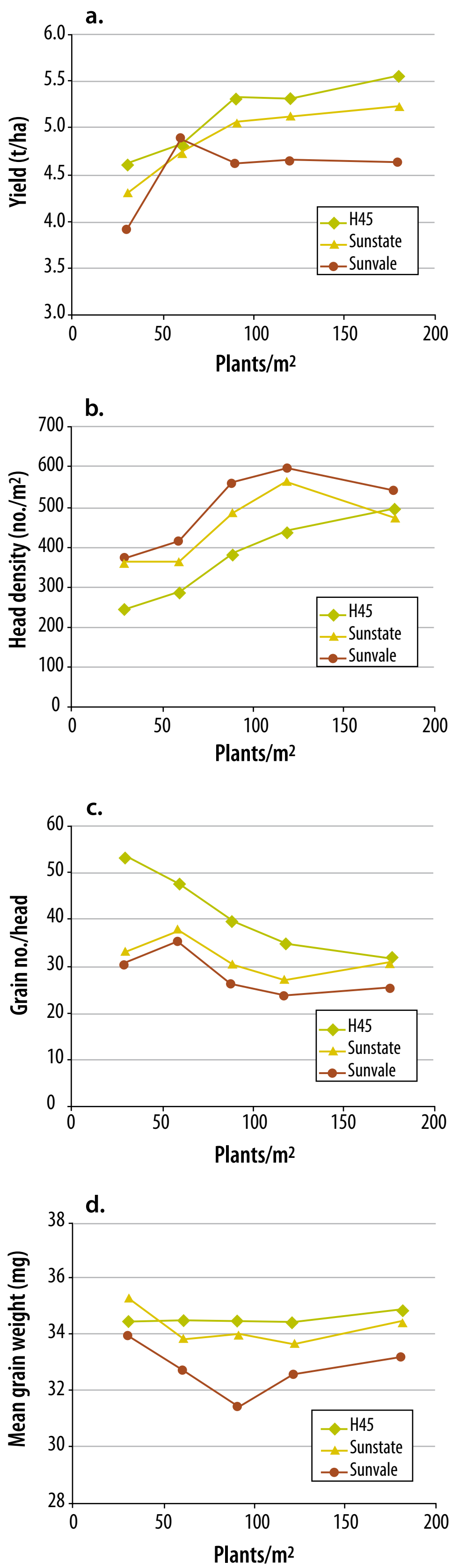
The trials showed that high plant populations (greater than 140 plants/m^2) do not necessarily lead to small grain or high screenings. The results also showed differences among the varieties in the way yield was achieved. The high yields of H45 were from a high grain number per head, even though it had lower tiller and head density at maturity.

The response to plant population was very different at Condobolin, where stored soil moisture and September rainfall were much lower. The results are presented in Figure 1–9.

Higher plant populations with the later flowering varieties led to excessive growth and water use prior to flowering, resulting in a low **harvest index**. The low harvest index was due to water stress around flowering causing a decrease in grain number, rather than a decrease in mean grain weight.

It is likely that post-flowering stress limited grain filling, and that there were not enough pre-flowering water-soluble carbohydrates to maintain grain size with the high grain number.

Harvest index
is a way of measuring the proportion of above-ground dry matter that is grain.



Grain yield

- H45 and Sunstate had similar responses to increasing plant density, with yield increasing up to 90 plants/m².
- Yield did not increase once densities were higher than 90 plants/m².

Head density

- In all varieties the number of heads/m² increased with plant population, from an average of 320 at the lowest plant population to up to 520 at the highest.

Grain number per head

- On average, there was a decrease in grain number per head from 40 to 30 with increasing plant populations, with an even larger decrease in H45, offsetting the increase in the number of heads/m².

Mean grain weight

- Plant population had little effect on mean grain weight which suggests that post-flowering conditions, possibly helped by stored carbohydrate, were adequate to fill all grains equally. The screenings values were less than 2%.

Figure 1–8: Effect of plant population in three wheat varieties on a) grain yield, b) head density, c) grain number per head and d) mean grain weight, Dubbo 2003.
Source: Based on N Fettell, 2006, 'Plant population responses in wheat', District Agronomist Technical Update, Orange.

Grain yield

- Grain yield was highest in the earliest-flowering lines (H45 and Hybrid Mercury).
- It decreased with increasing plant density in all varieties, particularly in the slowest-maturing variety (Sunvale).

Mean grain weight

- Plant population had little effect on mean grain weight.

Screenings

- Plant population had little effect on screenings.
- Screenings were greatest in H45 and Hybrid Mercury, the two varieties with the highest grain numbers.

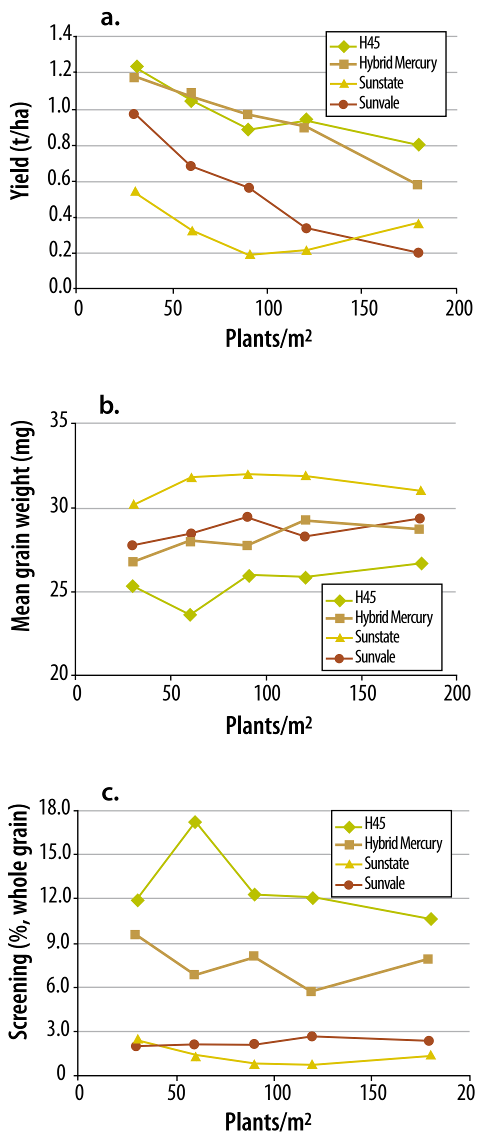


Figure 1–9: Effect of plant population in four wheat varieties on a) grain yield, b) mean grain weight and c) screenings, Condobolin 2003.
Source: Based on N Fettell, 2006, 'Plant population responses in wheat', District Agronomist Technical Update, Orange.

Seed storage

The aim of storage is to preserve the viability of the seed for future sowing and maintain its quality for market. A seed is a living organism that releases moisture as it respires. The ideal storage conditions are listed below.

- *Temperature below 15°C***.** High temperatures can quickly damage seed germination and quality.
- *Moisture control.* Temperature changes cause air movements inside the silo that carry moisture to the coolest parts of the seed. Moisture is carried upwards by convection currents in the air; these are created by the temperature difference between the warm seed in the centre of the silo and the cool silo walls, or vice versa. Moisture carried into the silo head space may condense and fall back as free water, causing a ring of seed to germinate against the silo wall.
- *Aeration* slows the rate of deterioration of seed with between 12.5% and 14% moisture. Aeration markedly reduces grain temperature and evens out temperature differences that cause moisture movement.
- *No pests*. Temperature below 15°C stops all major grain insect pests from breeding, slowing down their activity and causing less damage.

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IN THE PADDOCK

The following are some examples of what can be done in the paddock to demonstrate the stages of growth and development that have just been discussed.

1000-grain weight

Aim: to determine the 1000-grain weight of a seed lot.

1. Count out 200 seeds from each seed lot to be planted.
2. Discard seeds that will be removed by cleaning/grading.
3. Weigh 200 seeds on scales accurate to 0.1 g.
4. Multiply the result by 5 to calculate the 1000-grain weight.
5. Repeat 5 times.

1000-GRAIN WEIGHT (g)		
COUNT	SEED LOT 1	SEED LOT 2
1		
2		
3		
4		
5		
Average		

Graded versus ungraded seed

Aim: to compare a sample of a graded seed lot with one off the header.

1. Weigh out a small amount (e.g. 100 g) from both the graded seed lot and off the header.
2. Separate the plump, whole grains from the cracked and small grain, and the foreign bodies from the seed off the header.
3. Weigh each portion and compare the results.

Other suggestions:

Look at partial germination and seed that has been shot and sprung.

Calculating the germination percentage

Aim: calculate the germination percentage of a seed lot.

1. Collect 50 seeds from each lot to be planted.
2. Lay four sheets of paper towel on top of each other and moisten, don't drench.
3. Place 50 seeds 10 mm apart on the paper towels.

IN THE PADDOCK

4. Roll up, sandwiching the seeds between the moist paper towels.
5. Soak a hand towel in water and ring out, then wrap it around the rolled-up paper towel and loosely secure with rubber bands.
6. Place in a plastic bag, seal and place in a warm spot, such as the kitchen bench near a window, and leave for 5 to 7 days.
7. Unwrap and count the number of seeds that have not germinated.
8. Do your calculation as follows:

   Germination % = [(number of seeds tested – number of seeds that didn't germinate) ÷ 50] ×100.

9. Repeat five times.

GERMINATION PERCENTAGE		
COUNT	SEED LOT 1	SEED LOT 2
1		
2		
3		
4		
5		
Average		

Calculating sowing rates

Aim: calculate a sowing rate based on a target plant density.

1. Decide on a target plant density (refer to the *Winter crop variety sowing guide).*
2. Calculate the 1000–grain weight.
3. Use the following formula to calculate sowing rates:

$$\text{Sowing rate kg/ha} = \frac{(\text{target density} \times \text{1000-grain weight in grams} \div 100)}{(\text{establishment \%} \times \text{germination \%})}$$

COUNT	EXAMPLE 1	EXAMPLE 2	PADDOCK 1	PADDOCK 2
Target density	140	140		
1000-grain weight (g)	35	42		
Establishment	80% = 0.8	80% = 0.8	80% = 0.8	80% = 0.8
Germination	90% = 0.9	90% = 0.9		
Sowing rate	68	82		

IN THE PADDOCK

Coleoptile length and sowing depth

Aim: to measure coleoptile length and sowing depth. Plants need to be assessed at the one to two leaf stage.

1. Carefully dig up 10 plants along a row, including the seed and roots, in two paddocks.
2. Measure the depth from the seed to the soil surface—where the coleoptile ends and the green stem begins.
3. Record the coleoptile length of the 10 plants from each paddock in the table below and calculate the average sowing depth.

COLEOPTILE LENGTH / SOWING DEPTH (cm)		
COUNT	PADDOCK 1	PADDOCK 2
1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
Average		

Sowing implements and seed placement

Aim: to use coleoptile length measurements to compare the sowing depths of different tillage implements.

1. Conduct the above activity in paddocks that have been sown with different types of planters or in different soil types.
2. Discuss soil throw in zero till and implications for emergence.
3. Observe and discuss the impact of deep furrows on seed placement and emergence.

IN THE PADDOCK

Treated and untreated seed

Aim: to use coleoptile length measurements to compare treated and untreated seed.

1. Conduct the *Coleoptile length and sowing depth* activity at emergence in paddocks that have been treated with different seed treatments, and in paddocks where untreated seed was sown.

2. Record the coleoptile lengths of 10 seedlings from each paddock and compare results.

3. Compare emergence date of paddocks where treated and untreated seed was sown.

Plant population

Aim: determine the plant population in a paddock.

1. Count the plants along 1 m of row at 10 locations within the paddock.

2. Add the 10 counts together and divide by 10 to give the average number of plants/m of row.

3. Multiply the plant counts by the row spacing factor to convert plants/m row to plants/m^2.

17.5 cm = 5.71	20 cm = 5.00	33 cm = 3.03
22.5 cm = 4.44	25 cm = 4.00	36 cm = 2.77
27.5 cm = 3.36	30 cm = 3.33	40 cm = 2.50

4. Repeat in a different paddock and record the results for both.

PLANT POPULATION		
COUNT	PADDOCK 1	PADDOCK 2
1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
Total		
Average per m row		
Plants/ m^2		

2. Vegetative growth

by Andrew Schipp & Janet Wilkins

Chapter Snapshot

Introduction

Once the plant is established, it begins vegetative growth. Its root system continues to develop, leaves are initiated and tillering begins.

Chapter 2 explains vegetative growth and the factors that affect the growth and development of the plant.

Learning Outcomes

At the end of this chapter, you will be able to:

- identify the difference between growth and development
- describe how the root system grows
- understand the effect of vernalisation, photoperiod and thermal time on development in different varieties
- explain photosynthesis, respiration and transpiration
- understand how dry matter or biomass is accumulated
- describe the role of plant nutrition during vegetative growth
- locate the main stem and tillers of a wheat plant
- assess the dry matter or biomass of a crop.

Vegetative growth Z10–Z31

During the vegetative growth phase the roots, leaves and tillers grow and the plant begins storing nutrients for the rest of the life cycle. This is a period of high nutrient uptake, and its progression is influenced by moisture and temperature.

Growth is the increase in the size and number of leaves and stems, which produces more biomass. Growth is fuelled by photosynthesis and so directly relates to water use and light interception.

Development is the process of the plant moving from one growth stage to another. The rate and timing of plant development are determined by variety, photoperiod and temperature.

Root growth

The function of the root system is to absorb nutrients and water for plant growth. Healthy roots, unrestricted by soil constraints or disease, are essential to maximise yield. Roots also synthesise growth regulators or plant hormones.

Wheat has a fibrous root system consisting of two parts, the primary and secondary roots (Figure 2–1).

Primary root system (Z12)

The primary (seminal or seedling) roots are the first to appear after germination. The first primary (embryonic) root is followed by two other roots that grow on opposite sides of the first (see Figure 2–1). By the time the seedling is at the two-leaf stage the number of roots varies from two to five but most plants will have at least three roots. There can be as many as eight roots in the primary system, with up to three orders of branching.

These roots support the plant until the secondary roots appear. Primary roots can grow to a depth of 2 m. In most cases, the secondary root system takes over and becomes dominant. Where drought conditions prevent secondary roots from growing, the primary root system can support sufficient plant function to produce some grain.

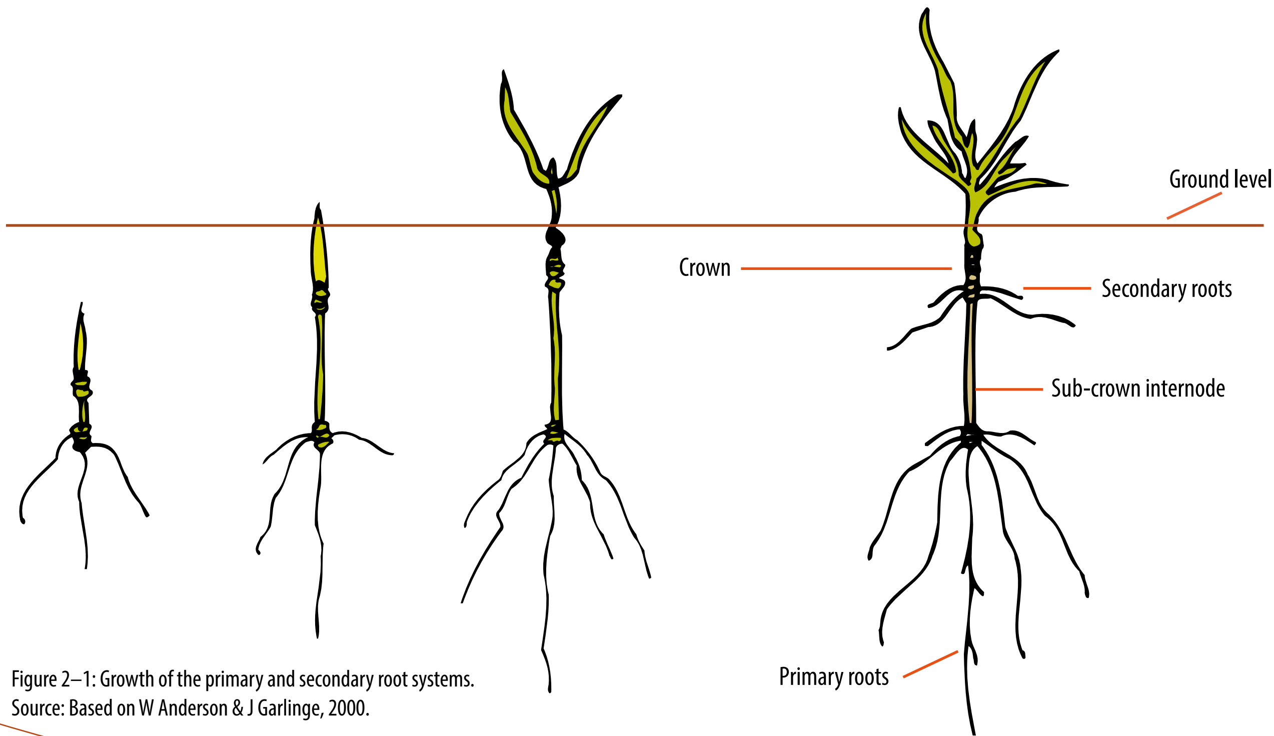


Figure 2–1: Growth of the primary and secondary root systems.
Source: Based on W Anderson & J Garlinge, 2000.

Secondary root system (Z13)

Secondary roots are also referred to as adventitious, nodal or crown roots. The secondary root system develops when the crop begins to tiller. These roots originate from both the tillers and the main stem and generally develop after a shoot has formed three leaves. The secondary roots are thicker than the primary roots and usually emerge horizontally. When they first appear they are white and shiny (see Figure 2–2), and are within 20 mm to 50 mm of the soil surface. For the main stem of the plant, these roots start to grow at the three to four leaf stage from the node above the primary system.

Root growth continues until flowering. As the root system matures it spreads and branches. Root branching occurs in a regular pattern in parallel with leaf growth.

The number of roots formed on a tiller is associated with the number of leaves. More leaves on a tiller means more roots, so the total root mass increases with the number of tillers.

Root volume

The wheat plant's fibrous root system develops horizontally and vertically, producing more surface area than plants with tap root systems. This is an advantage in less fertile soils, as it increases the chance of intercepting nutrients. Cereals often have a root surface area five to 10 times that of pulses, which may be an advantage in conditions where moisture is limited. Within the wheat family, bread wheats are thought to have a larger root system than durums and are therefore better able to utilise moisture and nutrient reserves in the subsoil.

The roots are covered in microscopic hairs that greatly increase the surface area of the roots. When root hairs are factored in, the root system of one plant may have a total absorbing surface area of hundreds of square metres.

Figure 2–2: Photo of a wheat plant, showing the primary and secondary root systems.
Photo: J Wilkins

Early sown crops are likely to have a more extensive root system than later sown crops simply because of the extra time available for growth. For example, the root system of winter wheat is often more extensive than that of shorter season spring wheats.

Vesicular–arbuscular mycorrhizae (VAM) provide a beneficial association between crop roots and soil fungi that occurs naturally in soils. VAM fungi help make soil nutrients—particularly phosphorus and zinc—available to a plant by acting as an extension of the plant's roots, increasing the volume of soil the roots can access. When wheat is grown in rotation with other crops, the VAM dependency of a crop becomes significant. Crops such as canola, with no VAM dependency, leave very low VAM levels in the soil for the following crop (see Table 2–1).

Crown
is the point where the root of a plant joins the stem.

Although wheat is generally considered to have a low dependency, yield has been shown to be reduced by low VAM levels. Trials on the Darling Downs in 2000 showed that clean fallowing or growing canola instead of other crops in the previous season resulted in lower numbers of VAM fungi in the soil and poorer root colonisation of the subsequent wheat crop.

Research has not found this response to VAM in southern New South Wales and Victoria. This is probably because of lower soil temperatures in autumn and winter that restrict the uptake of nutrients by the fungi.

Table 2–1: The dependency levels of common crops to VAM, and the effects of VAM on production.

CROP	MYCORRHIZAL DEPENDENCY	POTENTIAL YIELD LOSS %*	VAM LEVEL AFTER CROP
Linseed, Faba bean	Very high	>90	Low
Sunflower, Mungbean, Pigeon pea, Chickpea	High	60–80	High
Maize	High	60–80	Moderate
Sorghum, Cotton, Soybean, Sudan grass	Medium	40–60	Moderate
Field pea, Wheat, Triticale, Oats	Low	10–30	Low
Barley	Very low	10–30	Very low
Canola, Lupins	Nil	0	Very low

** without VAM in the soil.*

Source: Queensland Wheat Research Institute, Toowoomba 1996.

Rate and depth of rooting

Roots extend 50 to 100 mm in the first week after planting. The rate of growth then slows until Z13 (typically the 6-week stage, the start of tillering), with the roots reaching a depth of up to 300 mm. Growth then speeds up, and greatest soil penetration is achieved from Z13 to Z18 (typically 8 to 13 weeks after emergence). The roots penetrate downwards at a rate of about 10 to 15 mm per day, which equates to 1000 to 1500 mm root depth after 100 days (see Figure 2–3).

This pattern of growth means that root dry matter reaches a maximum at around the time of flowering. At maturity, 60% of the root system is within 300 mm of the **crown**. The maximum rooting depth depends on soil type and growing conditions. Depths of over 1700 mm, 10 to 14 weeks after planting, have been recorded on sandy loams.

The final rooting depth is normally determined by the depth of wetting during the growing season. This is often less than 1000 mm (1 m). There are a number of factors that can prevent roots from developing in the subsoil, including lack of moisture, chemical constraints such as salinity, acidity or high aluminium, and physical constraints such as soil density or compaction.

Lack of moisture is a very common reason for poor rooting depth. Roots can't grow through dry soil, so stored subsoil moisture can't be reached if a band of dry soil separates the roots from moisture. Where there is a chemical or physical constraint in the subsoil, moisture may be left in the profile at the end of the season. In dryland situations where roots can't penetrate into the subsoil, wheat plants can compensate to some extent by extending more roots in the surface soil.

Moist soil allows better penetration by the roots, so when moisture isn't limiting, roots are able to grow deeper provided there are no other barriers to growth. Plants that develop fewer deep roots have greater dependence on in–crop rainfall after flowering because stored moisture at depth can't be reached.

Roots branch profusely around moisture and sources of nutrients, especially phosphorus.

Leaf growth

All above-ground growth of the wheat plant, such as the leaves, stem and head, comes from a meristem (growing point). The main function of the leaves is to capture the energy of sunlight and, through photosynthesis, convert it to a form that can be used by the cells of the plant. (See *Photosynthesis and respiration* on page 33).

Leaf growth occurs between 0º and 38ºC, the optimum temperature being 29ºC. As temperature decreases, especially once it is below about 25 ºC, leaf growth slows. Each leaf has a phase of rapid expansion and unfolding. It takes about 110 degree-days for each leaf to unfold. So at 11ºC a leaf would take 10 days to unfold. A leaf is completely unfolded once the leaf collar is visible. At the optimum temperature leaf growth is rapid, associated with faster tillering, so crops that are sown early develop biomass at a more rapid rate. This is particularly important if the crop is being grazed, as biomass is needed early. (See *Thermal time* on page 41).

The final number of leaves for a spring wheat depends mainly on photoperiod, and for a winter wheat on vernalisation.

The rate of leaf growth is affected by variety, temperature, light intensity and nutrition. A plant has the genetic capacity to form up to 20 leaves, but generally five to nine leaves are found on the main stem.

Individual leaves have a limited life span. To compensate, the wheat plant has a mechanism for replacing older leaves. As leaves at the base of a stem die new leaves form and unfold higher up the plant.

Tiller growth (Z23–Z29)

The wheat plant produces additional shoots called tillers, some of which will produce a head. Tillers form from buds at the base (axil) of the leaves. The first tillers to emerge are formed between the axil of the coleoptile and the first true leaf.

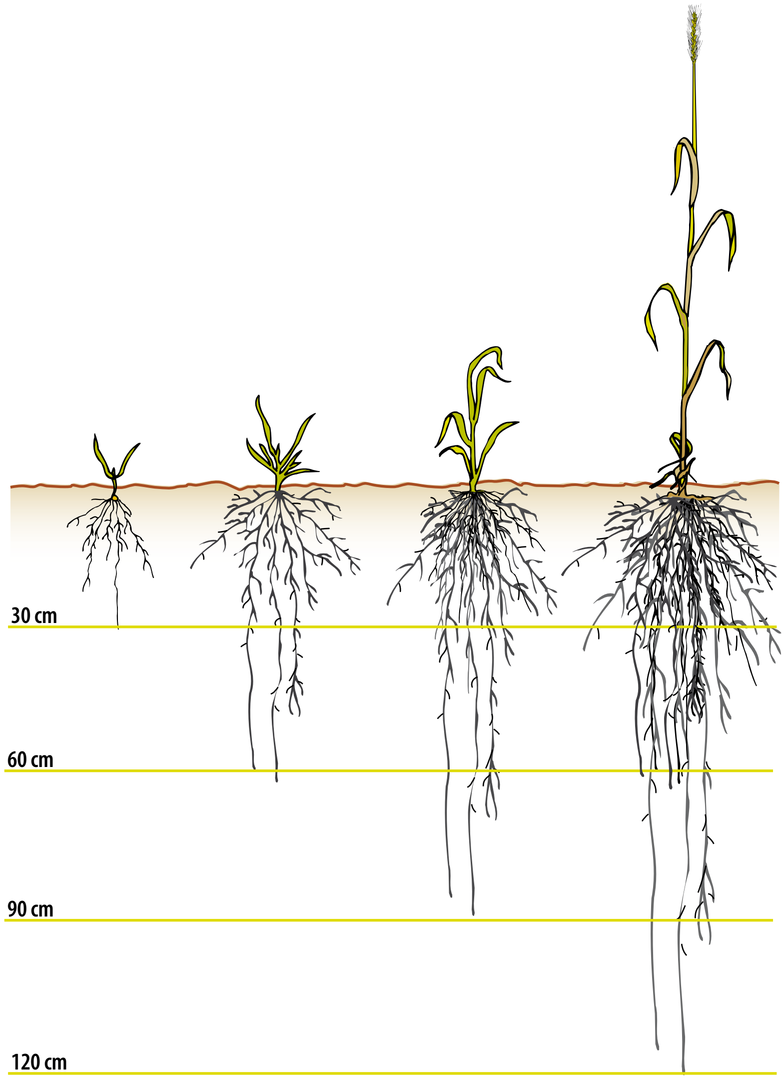


Figure 2–3: The increase in root volume as the wheat plant develops
Source: Based on J Weaver, 1926.

The appearance of these tillers coincides with the emergence of leaves on the main shoot. Tillering usually begins when the third leaf is fully expanded. Further tillers are produced in regular sequence so subsequent tillers emerge with the next leaf on the main stem.

Number of tillers

The number of tillers per plant depends on competition for growth factors such as water, nutrients and light. Tillering is very significant in agronomic terms.

Once the plant is established, it is a mechanism by which the wheat plant can compensate for low plant numbers. The ability to compensate with tillers depends on variety, the availability of nutrients, especially nitrogen, and seasonal conditions.

Different varieties have different tillering capacities. Some may have only four or five tillers per plant, while others can have as many as 80. H45 is an example of a variety with few tillers, while Sunvale produces a greater number of tillers. (See *Tillering capacity* on page 37).

Plant population, sowing date and nutrition are factors that can be managed to achieve a desired tiller density. Generally, increasing seeding rates, and therefore increasing plant density, usually reduces tiller number per plant, with the reduction depending on the variety and the size of the increase in seeding rate. However, research indicates that this is not always the case. Similarly, reducing plant density usually increases the number of tillers.

Tiller mortality

Not all of the tillers produce a head. A number die off, depending on the resources available to the plant, the later-formed tillers usually dying first. Surviving non-productive tillers provide nutrient and carbohydrate reserves for grain-bearing tillers. Figure 2–4 shows the tiller mortality in four varieties sown at Cowra in 2002. Sunvale maintained tillers even with a higher plant density, while Wedgetail and H45 dropped tillers.

End of tillering (Z29)

Under optimal conditions, it is competition for light as the canopy closes that causes tillering to stop. This is generally at 50% to 60% light interception. The growth stage reached at the end of tillering depends on the variety. In late-maturing varieties (generally winter wheats), tillering ends when the plant is at the double ridge stage. Tillering stops in early-maturing varieties (spring wheats) after the terminal spikelet stage (Z30). Tillering may also continue until Z30 in crops with low plant density, allowing for some compensation in tiller number and therefore yield. (See also *Chapter 3: Reproductive development*).

Factors affecting vegetative growth

Prior to establishment, plant growth is fuelled by energy reserves stored in the endosperm of the grain. Once the first two leaves have unfolded, growth relies on energy produced by the plant through photosynthesis.

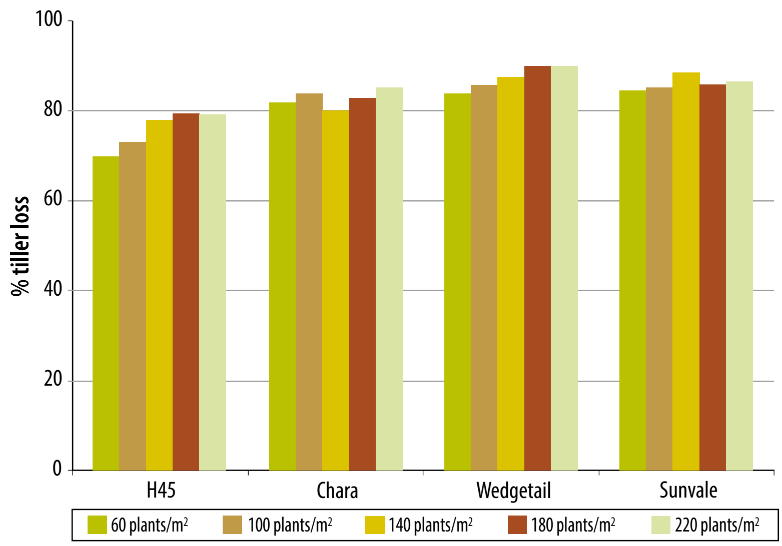


Figure 2–4: Tiller mortality per m^2 at Cowra.
Source: NSW Department of Primary Industries, Plant population project 2002.

- Tiller mortality is influenced by variety and plant population
- Sunvale maintains its tiller number with increasing plant density
- H45 and Wedgetail have a higher tiller mortality as plant density increases.

Photosynthesis and respiration

Plants get their energy to grow from sunlight captured by the leaves. Photosynthesis is the process by which plants use this energy to convert carbon dioxide to sugars (Figure 2–5). The sugars are converted to cell wall-forming substances that make up leaves, stems, roots and other plant parts. Excess sugars are stored as water soluble carbohydrates.

When energy can't be obtained from sunlight, such as at night, the plant draws on its reserves of starch and sucrose. This process is called respiration.

The rate at which the plant grows is closely linked to the amount of sunlight being captured by the leaves. Temperature influences the rate at which the chemical reactions of photosynthesis occur. The ideal temperature range for wheat plants is from 15° to 30°C.

How efficiently a leaf photosynthesises is determined by factors such as variety and nutrition. For example, wheat plants that are nitrogen deficient have yellow stunted leaves. Small leaves simply catch less light, and yellow leaves have less chlorophyll, the pigment responsible for capturing the sunlight energy.

Transpiration

Plant water use or the evaporation of water from within a leaf is called transpiration. During transpiration, water evaporated from the wet cell walls within the leaf moves into the leaf airspaces and out through the leaf stomata.

Transpiration and photosynthesis are related. Leaf stomata need to be open to allow water vapour to move out and to allow carbon dioxide for photosynthesis to move in. When plants are transpiring, water is drawn up from the soil all the way to the leaves to replace the water lost to the atmosphere.

Transpiration is slower in cool conditions with high humidity, and faster in windy, hot conditions with low humidity.

Photosynthesis equation

$$6CO_2 + 6H_2O \xrightarrow{\text{light}} C_6H_{12}O_6 + 6O_2$$

carbon dioxide + water → carbohydrate + oxygen

Respiration equation

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{energy}$$

carbohydrate + oxygen → carbon dioxide + water + energy

Figure 2–5: Equation for photosynthesis and respiration.

These hot conditions are unfavourable when combined with low soil moisture because as the soil moisture drops, the stomata close to conserve moisture and photosynthetic productivity is lost.

Leaf area

The photosynthetic capacity of the crop is related to the total leaf area and the length of time this area is maintained. Maintenance of the leaf area is essential for the production of the carbohydrates used during grain filling.

Leaf area is influenced by the rates of leaf appearance, tiller production and leaf expansion.

Leaf area is measured by the leaf area index (LAI), the amount of leaf area in a crop canopy. If a square metre of crop is cut at ground level and the leaves are laid out flat, touching each other with no gaps, the area covered is the leaf area index. So if the leaves covered 3 m^2, the crop has a LAI of 3.

The LAI of a crop determines water use. The higher the LAI the more water used during the vegetative growth stage. In dryland crops, a large area of leaf in early vegetative growth may use water needed for flowering and grain fill. So a balance needs to be reached between a large leaf area to maximise photosynthesis and the production of carbohydrate, and maintaining sufficient soil moisture for grain fill.

Stomata
are tiny pores on the leaves
that allow gas exchange.

Moisture

Availability of soil moisture affects the rate of transpiration and photosynthesis.

Moisture stress

Moisture stress slows photosynthesis and leaf area expansion, reducing dry matter production. It also limits root growth, thus reducing nutrient uptake. This is significant for areas with low rainfall. The period of crop growth is restricted at the start of the season by lack of rainfall and at the end of the season by water deficits and high temperatures. There is little scope in the low rainfall areas of the wheat belt to lengthen the period of crop growth to increase dry matter production and yields.

Waterlogging

Wheat is sensitive to waterlogging. It causes low soil oxygen concentrations, which limit root function and survival.

The availability of nitrogen and other nutrients may be reduced by waterlogging, slowing the rate of leaf growth and accelerating leaf death. Tiller initiation also slows, reducing the growth and survival of tillers. This reduces yield, with the amount depending on the growth stage at which waterlogging occurs.

As waterlogging typically occurs in winter, it is an issue in southern New South Wales, where most of the rainfall is received in winter.

Nutrition

Nutrition affects the rate of plant growth. Nutrients need to be supplied within an optimum range from germination onwards to maximise plant growth. Nutrients are divided into two main groups: macronutrients required in large amounts by the plant, and micronutrients required in small amounts.

Most nutrient uptake is through the root system. Intake of nutrients through the leaves is usually insignificant, apart from a few minor nutrients such as copper, zinc, manganese and molybdenum. Using these nutrients as foliar sprays before flowering can increase yields where crops are deficient.

The mobility of nutrients in the soil determines the way plants take them up. This has implications for the use of fertilisers and their placement in the soil. Nutrients that are soluble and therefore mobile are transported through the root system by mass flow from transpiration. These nutrients include nitrate, calcium, magnesium and sulfate.

Less mobile nutrients such as potassium move to plant roots along a concentration gradient by a process called diffusion. The nutrients move from a high concentration area in the soil to a low concentration area around the plant roots. For plants to take up nutrients that have low mobility in the soil solution, such as phosphorus, copper and zinc, the roots need to grow through the soil in contact with the nutrients.

Table 2–2: Nutrient removal (kg) for each tonne of wheat or cereal hay.

	WHEAT GRAIN CLASSIFICATION				DURUM WHEAT	CEREAL HAY
	PRIME HARD	AUST. HARD	ASW*	ASW* SOFT		
Nitrogen	24.5	2.43	3.10	1.64	0.36	1.64
Phosphorus	21.8	2.26	3.33	1.4	0.33	0.93
Potassium	17.7	2.41	3.4	1.35	0.31	1.02
Sulfur	16.6	2.51	3.43	1.19	0.32	0.95
Calcium	23.1	3.09	4.34	1.52	0.37	0.99
Magnesium	20	2	12	1.5	12	3

** Australian standard white*

Source: G Price, 2006.

In considering crop nutrition it is important to take into account nutrient removal from the previous crop. Table 2–2 shows the amount of nutrients removed in each tonne of wheat. Crop management can also affect nutrient removal, and high levels of some nutrients can be lost through stubble burning (Table 2–3).

Table 2–3: Stubble nutrients lost from a hot burn (for a wheat crop yielding 5 t grain per ha and 7.5 t stubble per ha).

NUTRIENT	AMOUNT OF NUTRIENTS IN STUBBLE (kg / ha)
Nitrogen	56
Phosphorus	5.9
Potassium	109
Carbon	3450

Source: Australian Farm Journal, December 2003.

Nitrogen

Nitrogen supply influences nearly all components of the growing wheat plant, so it needs to be available right through the growing cycle to achieve good yield and grain quality. In intensive cropping systems, nitrogen is the nutrient that most commonly limits crop production.

During vegetative growth nitrogen is required for root growth, leaf growth, tillering and the production of chlorophyll. Nitrogen readily moves within the plant to areas of active growth. For this reason nitrogen deficiency symptoms first appear as yellowing of the older leaves, as nitrogen is translocated to the younger actively growing tissues.

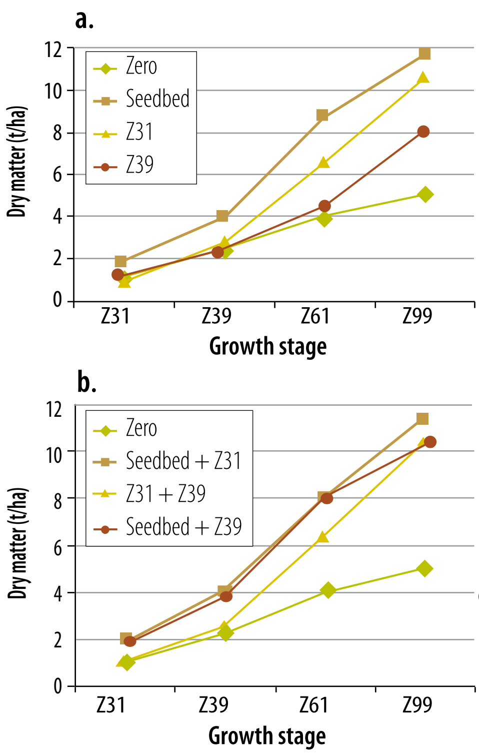
Nitrogen supply and light intensity control the rate and pattern of growth of an individual tiller. Where there is adequate nitrogen and light a tiller grows continuously. Where light or nitrogen are limiting, growth is not continuous and instead occurs in intervals.

Nitrogen nutrition is slightly more complex than other nutrients, because there is a strong connection between plant growth, nitrogen supply and available soil moisture. This is particularly important in dryland situations.

In medium to high rainfall areas, a tactical approach to nitrogen application may be best. The idea is to apply enough nitrogen to achieve a 70% yield potential with a reasonable protein level (11% to 12%). If the season turns dry, resources have not been wasted, because of the large biomass from nitrogen application and the fact that soil moisture is conserved for grain fill. If good soil moisture continues into late tillering, then the option of nitrogen topdressing is available.

There are risks associated with large applications of nitrogen. If the season turns dry, the crop has used soil water growing the large biomass. Without good rainfall there is a risk of haying-off.

Early applications of nitrogen increase the production of biomass or dry matter (see Figure 2–6 a & b), which increases yield (provided there are sufficient resources to support it). Wheat plants that receive excessive levels of nitrogen early in the season (Z20 to Z39) produce a large number of tillers that may not be sustainable because of the amount of water required by the large leaf area.



- More dry matter was produced with all nitrogen treatments.
- The greatest increase was when nitrogen was applied at sowing and Z31.

Figure 2–6: Influence of nitrogen timing on dry matter production (t/ha), a. single nitrogen doses, b. split nitrogen doses, assessed at Z31, Z39, Z61 and Z85–Z90. Source: Based on N Poole et al., 2007.

Adequate nitrogen in the later stages of growth increases the length of time the canopy stays green, provided moisture is not limiting, and thus maximises photosynthesis. For this reason crops that are not grazed have lower levels of nitrogen applied at sowing and are topdressed (depending on seasonal conditions) prior to Z31. This approach is mainly used in areas of New South Wales where there is reliable growing season rainfall or irrigation. Topdressed nitrogen needs to be applied just prior to a rain front or through irrigation for it to be used efficiently. (See *Chapter 3: Reproductive development, Nitrogen*).

Phosphorus

Phosphorus is essential for almost every plant function. During vegetative growth it is essential for the energy storage and transfer system of plant cells and is needed for the rapid cell division and expansion taking place.

Phosphorus is not mobile, so roots need to be in direct contact with it in the soil. The amount of phosphorus available depends on the soil type, as phosphorus reacts with the soil in a complex way. As it comes in contact with the soil it can become chemically bound into the soil, with as much as 50% converting to forms unavailable to the plant. This needs to be taken into account when determining the rate of application.

Phosphorus needs to be supplied in the root zone for it to be taken up by the plant, so its uptake is closely associated with root depth. Fertiliser placement and depth below the seed are important, particularly in no-till situations.

Symptoms of phosphorus deficiency in wheat are usually non-specific and difficult to diagnose. As phosphorus is needed for cell division, wheat plants suffering severe phosphorus deficiency are slower to reach each growth stage. These plants tend to put more resources into root growth rather than shoots in the search for more phosphorus. Tiller production is restricted, as is the rate of appearance of new leaves. The deficient crop has a reduced height and grain yield. Leaves also become dark green.

Phosphorus deficiency leads to poor uptake of other nutrients and reduces water use efficiency and drought tolerance.

Potassium

Potassium is a major plant nutrient, required in similar amounts to nitrogen. It is used in many plant processes, including photosynthesis, transport of sugars and enzyme activation. Potassium is particularly important in the regulation of stomata in the leaves. So plants that are deficient in potassium can't use other nutrients and water efficiently. They are less tolerant of stresses such as drought and waterlogging.

Potassium, unlike nitrogen and phosphorus, is adequate in most Australian soils, so a deficiency is rarely seen. Potassium is very mobile in plant tissues. In deficient plants it is moved to new growth, so deficiency symptoms appear first in older leaves. The symptoms are yellowing and death (necrosis) of the tips of the oldest leaves. In wheat the necrotic areas can have a red appearance.

Sulfur

Sulfur is part of every living cell and is an element of three of the 21 amino acids that form proteins. Sulfur deficiency in wheat is rarely seen, but where high analysis fertilisers are used sulfur levels can become low enough to restrict growth. Sulfur is not mobile in the plant tissues, so deficiency symptoms appear first as pale younger leaves. Growth and maturity is also slowed. With severe deficiency the whole plant becomes yellow and the stems turn reddish.

Micronutrients

There are a number of micronutrients essential to plant growth. They include molybdenum, zinc, copper, manganese and boron. With any of these nutrients there is a fine line between adequate nutrition and toxicity. Deficiencies are not common but when they occur yield loss can be substantial. Symptoms are often hard to diagnose and require a tissue test to confirm.

Molybdenum is essential for plants to use nitrate nitrogen and is required in cereals for grain formation. The heads of plants deficient in molybdenum are often empty or have shrivelled grain. As molybdenum is important in nitrogen metabolism, deficiency can initially look to have the same symptoms as nitrogen deficiency. Molybdenum is less soluble in acidic soils, so deficiency is more likely to be seen in these soils. Molybdenum is taken up early by the plant, and seed coatings can be sufficient to address deficiencies.

Manganese is required for many metabolic processes in the plant, including chlorophyll production. It is relatively immobile in the plant. Manganese toxicity is more common than deficiency, particularly in waterlogged soils. It appears as yellowing of the leaf margins but is more common in crops such as canola. A planned foliar spray rather than treating seed is a better strategy for an expected deficiency.

Zinc is involved in the enzyme systems of plants. Zinc deficiency usually shows as a pale area in the middle of the leaf extending towards new growth. It looks like a long, pale green strip on each side of the mid vein of the leaf and is more common in waterlogged or alkaline soils. Zinc blended with compound fertilisers used to supply phosphorus and nitrogen is the most common method of supplying it to wheat crops.

Copper is also essential in many plant enzymes and for lignification that gives a plant its structural strength. Copper-deficient plants can have weak stems and limp leaves. Copper deficiency also affects pollen production. Grain filling is restricted, as pollen sterility causes uneven or failure of grain set. Copper deficiency can be confused with moisture stress, frosting or molybdenum deficiency symptoms. Copper is in most demand by the plant from tillering onwards, so applying copper to seed is not usually recommended. Copper is usually applied as part of a blended fertiliser or as a foliar spray.

Tillering capacity

Varieties have different tillering capacities and this affects the target plant density. To achieve target tillers per plant, low-tillering varieties (such as H45) are best sown at higher plant densities than high-tillering varieties (such as Sunvale).

The results of a 2002 trial in Cowra demonstrate the tillering capacities of different varieties (Figure 2–7). At the lowest plant density, Sunvale produced 16 tillers/plant while H45 produced 6 tillers/plant.

- Tillers/plant is affected by variety and sowing rate.
- H45 is a low-tillering variety. Tillers/plant does not increase significantly with a low sowing rate.
- Sunvale is at the other extreme, showing a significant increase in tillers/plant as sowing rate decreases.

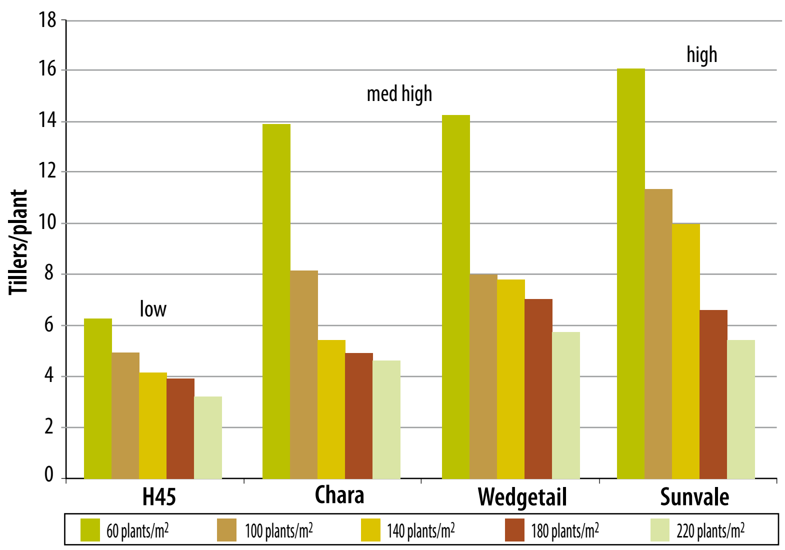


Figure 2–7: Tillers per plant of four wheat varieties at Cowra. Source: NSW DPI, Plant population project 2002.

Target tiller numbers relate to the number of tillers that can be sustained to produce optimum yields. The target is often related to rainfall. For example, target tiller number for a 500 mm rainfall zone is approximately 500 tillers/m^2.

Target tiller numbers for current varieties in New South Wales can be estimated by looking at the desired final yield and the amount of grain produced per tiller. Average yields vary from 0.8 g per tiller to 1.2 g per tiller. Varieties like H45 that have higher numbers of grain per head, and in good seasons produce bigger grains, are at the upper end of the weight (1.2 g per tiller) while varieties like Sunvale are at the lower end (0.8 g per tiller).

As an example, if the target yield is 3 t/ha, using a tiller grain weight of 1 g, 300 tillers/m^2 are required. If the variety is H45, slightly fewer tillers (250) are needed because the grain weight is higher per tiller. If the variety is Sunvale, around 370 tillers/m^2 are needed. Ventura produces 1.2 g of grain per tiller, so it needs fewer tillers. Ellison is similar. Carinya is similar to Janz, with around 1 g grain per tiller.

Wheat can partly compensate for high or low plant populations by dropping tillers or increasing grain numbers. However, targeting a variety's optimum plant number at sowing makes the most efficient use of available water and nutrients, which are otherwise used in this compensation process.

In dryland situations, at least 100 heads/m^2 is required for each tonne of yield per hectare. Typically, 70% to 75% of tillers go on to produce a head, so for a target yield of 5 t/ha, 650 to 700 tillers/m^2 may be needed by the end of tillering.

Research on irrigated wheat in New South Wales, targeting 8 t/ha of yield, has shown that this high level of yield is achievable if tiller numbers at Z30 are in the 500 to 800 tillers/m^2 range. Under irrigation and therefore absence of moisture stress, more tillers are likely to go on to produce heads. Spikelet number per head can also be maximised if there is sufficient soil moisture. For crops with tiller numbers at the lower end of the 500/m^2 to 800/m^2 range, nitrogen topdressing is necessary to ensure tiller survival and maximum grain number per head. (See *Nitrogen* on page 35).

Remember when calculating tiller numbers for topdressing at Z30 that 20% to 30% of tillers will not produce grain at maturity. For example, if the target is 500 to 600/m^2 tillers at maturity, 600 to 700/m^2 tillers are needed at Z30. (See *Chapter 3: Reproductive development, Nitrogen*).

Leaf and root disease

Paddock selection and rotation combined with disease-resistant varieties are the best actions to minimise disease. Foliar fungicides can also be used to treat leaf disease. A table of disease ratings for current varieties can be found in *Winter crop variety sowing guide.*

Disease can affect the growth and development of a wheat plant. Nutrient deficient plants are less resistant to pests and diseases.

Root diseases such as rhizoctonia, crown rot, and take- all can affect wheat in its early growth stages. When root disease occurs, the plant has less ability to absorb nutrients and water, so growth is restricted.

If the leaves are diseased the ability to photosynthesise is reduced. Foliar diseases such as wheat streak mosaic virus and stripe rust are more likely to be seen in crops that are sown early, when the weather is warmer.

Grazing

In mixed farming systems, it is common practice to graze wheat crops to fill the winter feed gap. Winter wheat varieties can be grazed without a major grain yield penalty provided they are not grazed after their vernalisation period has been met. Wheat crops can be grazed from 8 weeks after sowing, depending on the season.

Winter wheats are valuable because of the amount of dry matter (DM) or biomass they can produce. At Grenfell in 2004, the variety Wedgetail had a growth rate of 160 kg DM/ha per day, just prior to grazing (Figure 2–8). At Yerong Creek in the same year, the growth rate was 100 kg DM/ha per day just prior to the second grazing. These growth rates are three to four times greater than those of perennial pastures.

Grazing may reduce the water use of a crop. When the vegetation is removed, water is conserved in the profile for use during grain fill, mainly because there is less dry matter to transpire. In dry years grazed crops have out-yielded ungrazed crops sown at the same time. (See *Chapter 3: Reproductive development, Grazing*).

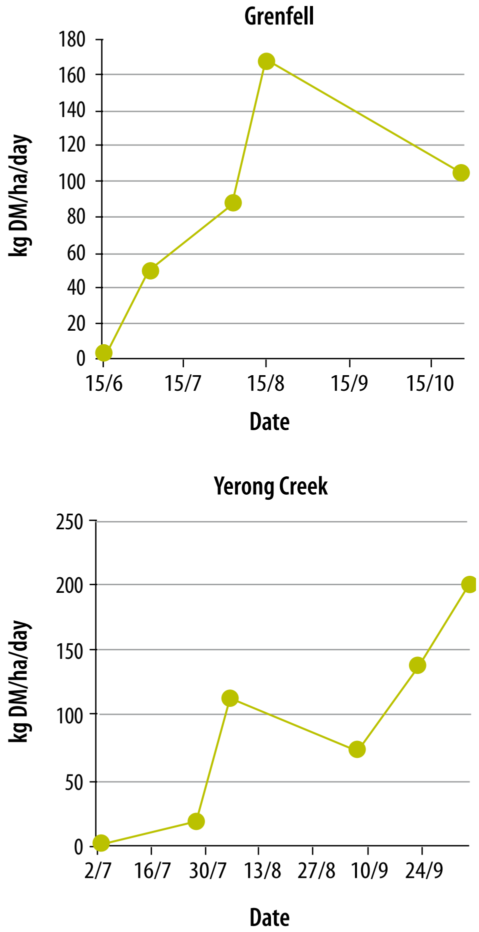


Figure 2–8: Growth rate of the variety Wedgetail at Grenfell and Yerong Creek in 2004.
Source: Based on J Virgona, F Gummer & J Angus, 2006.

- Growth rates just prior to grazing were 160 kg DM/ha per day at Grenfell and 100 kg DM/ha per day at Yerong Creek.
- The Grenfell site was grazed from 25–29 August and Yerong Creek from 10–13 July.

Factors affecting plant development

The main stem of the wheat plant determines the timing of plant development. The rate at which a wheat plant develops or moves from one growth stage to the next sets the limit for canopy growth and ultimately yield. The major factors affecting the length of each growth stage are vernalisation, photoperiod, thermal time and plant maturity. The significance of these factors depends on whether the wheat is a spring or winter type.

Leaf and tiller appearance, senescence (the aging and drying of leaves and non-productive tillers) and plant height are components of the canopy structure that, under non-limiting water and nutrient conditions, are determined by genotype and sowing date.

Vernalisation

Winter wheats have a vernalisation requirement that needs to be met before they switch to the reproductive phase. The length of the vernalisation requirement varies with variety (see estimates in Figure 2–9). For example, winter wheat

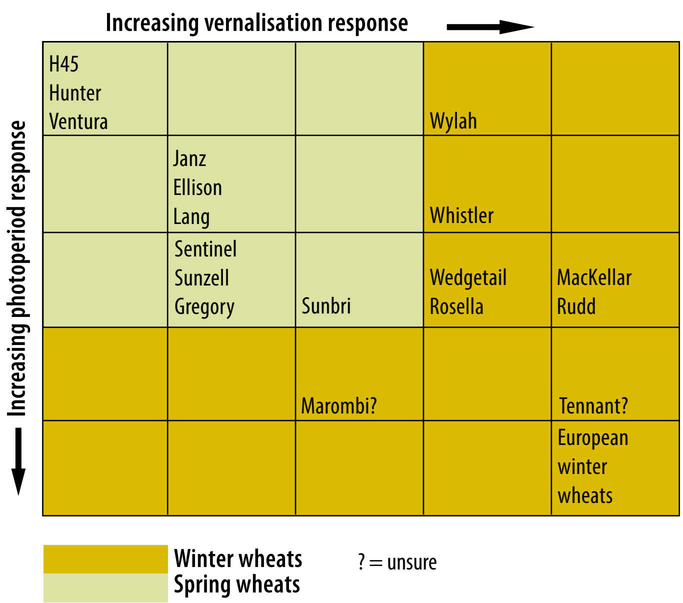


Figure 2–9: Estimated response of wheat varieties to vernalisation and changes in photoperiod. Source: P Martin (pers. comm.), 2007.

varieties such as EGA_Wedgetail and Whistler have a low vernalisation requirement so are grown in shorter season environments. Varieties that require a longer vernalisation period such as Rudd and MacKellar are grown in longer season environments such as the Tablelands.

Sowing date has less effect on flowering date in varieties that require vernalisation. These varieties are safer to use for early sowing than spring wheats (which do not have a vernalisation requirement) as they do not go to head until their cold requirement has been met. This reduces the risk of frost damage at flowering and grain fill.

The growing point of winter wheats remains in the crown or below the soil level until the vernalisation requirement has been reached, which is why they are used as grazing wheats. Tiller death is minimal provided grazing is stopped once the vernalisation requirement has been met. (See *Chapter 3: Reproductive development, Grazing*).

Photoperiod

Photoperiod or day length is the number of hours of daylight. Wheat is a long-day plant, meaning that it responds to increasing photoperiod. This sensitivity determines whether the plant continues to produce leaves or changes to reproductive development.

Photoperiod can affect the development of wheat by:

- causing changes in the rate of leaf area expansion and dry matter production
- providing a cue for the start of reproductive development
- changing the rate of reproductive development.

Spring wheats rely solely on photoperiod to trigger the reproductive phase. They are grown in short days of winter to mature in early summer as photoperiod increases.

Some winter wheats are photoperiod sensitive once their cold requirement has been met.

Varieties respond differently to photoperiod (see Figure 2–9). Understanding the photoperiod requirement of a variety helps explain recommended sowing windows. Varieties that require a long photoperiod to reach maturity, such as Gregory, are sown earlier. Short season varieties that require a short photoperiod, such as Ventura, are sown later.

Thermal time

Thermal time is a calculation of accumulated temperature. It helps to explain the relationship between plant development and temperature. It is calculated as the mean daily temperature minus a base temperature and is recorded as degree-days (°Cd). The base temperature is the minimum temperature at which the plant grows, and this varies for each crop. For wheat, the base temperature is 0°C during vegetative growth and 3°C in the reproductive phase. Table 2–4 lists the degree-days required for each growth stage. (See *In the paddock: Thermal time* on page 50).

Table 2–4: Generic growing degree-days required for each growth stage.

GROWTH STAGE	DEGREE-DAYS
Seedling to emergence	100
Emergence to first tiller	200
First tiller to single ridge	180
Single ridge to double ridge	125
Double ridge to terminal spikelet	150
Terminal spikelet to jointing	105
Jointing to flag leaf	300
Flag leaf to heading	140
Heading to anthesis	75
Anthesis to maturity	800
Maturity to harvest ripe	300
Total	2475

Although not commonly used at farm level, thermal time is very important for predicting the growth stages of some crops. It is not always a good predictor for wheat, as development is also influenced by photoperiod and vernalisation. In general, higher temperatures accelerate development between germination and flowering. However, under increasing photoperiod, thermal time has less effect on plant development.

While the rate of development may be controlled by many factors, higher temperatures and increasing photoperiod reduce the number of days in all growth stages. This is particularly important up until the flowering stage. There is a variation in thermal time between seasons (see Figure 2–10).

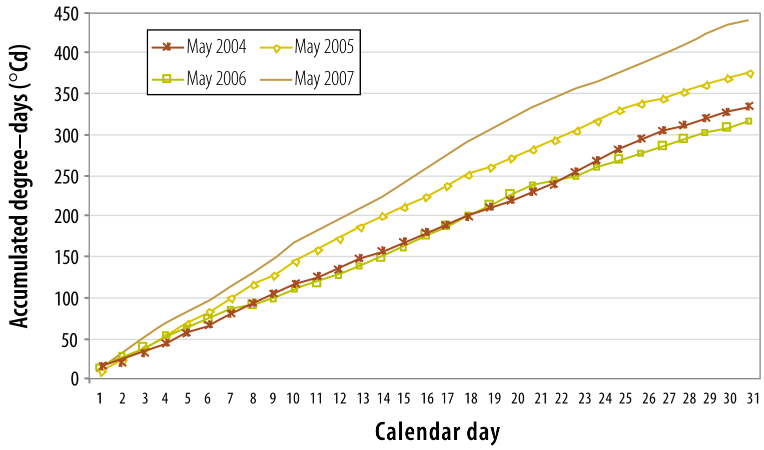


Figure 2–10: Variation in the thermal time across 4 years for the month of May at Cowra. Source: J Edwards, District Agronomist, Cowra 2007.

- Thermal time varies among years.
- 2007 accumulated nearly 450°Cd during May, compared with less than 350°Cd in 2004 and 2006.

Plant maturity

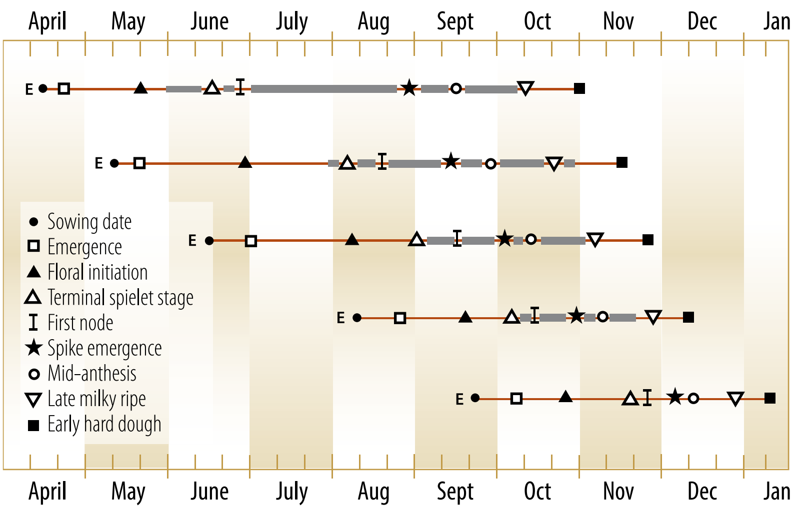
The maturity, or length of time taken for a variety to reach flowering, depends on vernalisation, photoperiod and thermal time requirements. Recommended sowing times are arrived at by assessing the maturity of varieties in different environments and with different sowing times. Figure 2–11 shows the variation in development stages when a variety is sown on different dates.

The maturity of varieties available in New South Wales varies greatly, and consequently there is a range of optimum sowing times. Table 2–5 is an example of the sowing window for a number of varieties in southern New South Wales. Up-to-date tables are published each year in the *Winter crop variety sowing guide*.

Sowing a variety outside of the sowing window increases the risk of flowering occurring at the wrong time, leading to frost damage or high temperatures at flowering and grain fill. Trials in northern New South Wales showed reductions in relative grain yield of 5% to 7% for each week that sowing was delayed after the end of June. (See *Chapter 3: Reproductive development, Flowering time*).

In sowing time trials conducted throughout the State, the response of four varieties to different sowing time was measured (see Figure 2–12). The results showed variations in yield stability for different varieties over a range of sowing times.

The data shown in the graphs does not include any allowance for risk of frosting from sowing early maturing varieties ahead of time. This should be taken into account when selecting an appropriate variety for the season or region.



- The length of the development stages changes with different sowing times.
- The average growing period was halved from 208 days for April to 100 days for September sowing.

Figure 2–11: The change in development stages and the duration of the growing period in 1983 for five different sowing times for Egret, a Janz type. The thick line indicates a period of full cover.
Source: Based on M Stapper & R Fischer,1990a.

Table 2–5: Recommended sowing times for varieties in southern New South Wales.

SLOPES

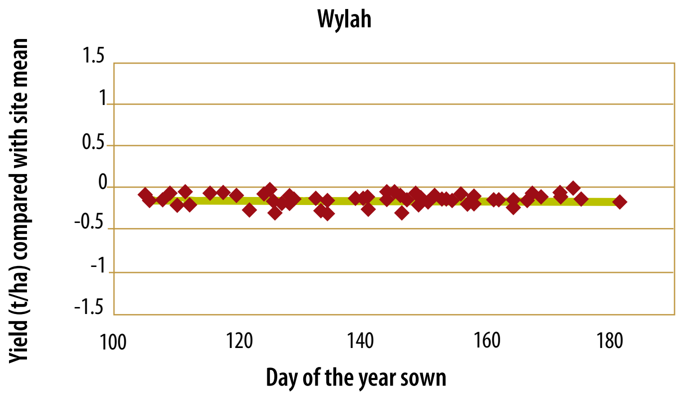
VARIETY	APRIL				MAY				JUNE				JULY		
WEEK	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3
Tennant, Brennan, Mackellar, Marombi, Rudd, Currawong, EGA_Wedgetail	>	★	★	★	★	★	<								
Sunbrook		>	★	★	★	<	<								
Sunbri, Braewood			>	★	★	★	★	<	<						
Sunlin, Strzelecki, Sunzell, Giles, EGA_Burke, EGA_Gregory, Sentinel				>	★	★	★	★	<						
EGA_Wylie, Sunvale, Ellison, GBA_Ruby, Sunco, Lang, GBA_Sapphire, Carinya, Hybrid Apollo					>	★	★	★	★	★	<				
Baxter, Petrel, EGA_Wentworth						>	★	★	★	★	<	<			
Kennedy, Ventura							>	★	★	★	★	<	<		
EGA_Bellaroi, Yallaroi, Wollaroi							>	★	★	★	★	★	<	<	
GBA_Hunter, H46, Jandaroi								>	★	★	★	★	<	<	

PLAINS

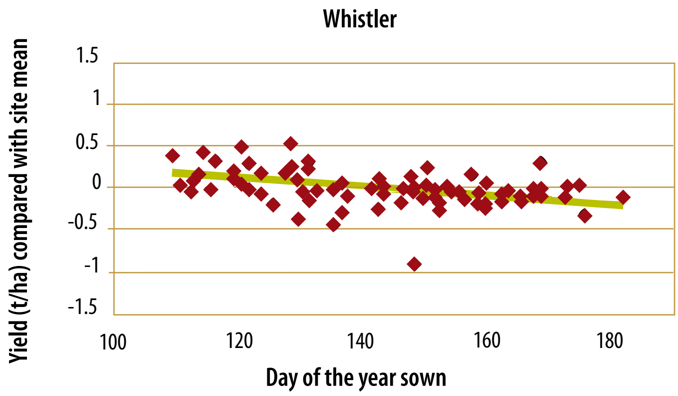
VARIETY	APRIL				MAY				JUNE				JULY		
WEEK	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3
Currawong, EGA_Wedgetail	>	★	★	★	★	★	<								
Sunbrook		>	★	★	★	<	<								
Sunbri, Braewood		>	>	★	★	★	★	<	<						
Sunlin, Strzelecki, Sunzell, Giles, EGA_Burke, EGA_Gregory, Sentinel				>	★	★	★	★	<						
EGA_Wylie, Sunvale, Ellison, GBA_Ruby, Sunco, Lang, GBA_Sapphire, Carinya, Hybrid Apollo					>	★	★	★	★	★	<				
Baxter, Petrel, EGA_Wentworth						>	★	★	★	★	<	<			
Kennedy, Ventura, EGA_Bellaroi, Yallaroi, Wollaroi							>	★	★	★	★	<	<		
GBA_Hunter, H46, Jandaroi								>	★	★	★	★	<	<	

> Earlier than ideal, but acceptable. ★ Optimum sowing time. < Later than ideal, but acceptable.
Petrel sown in late May for hay/chaff production. May be sown earlier if grazed.

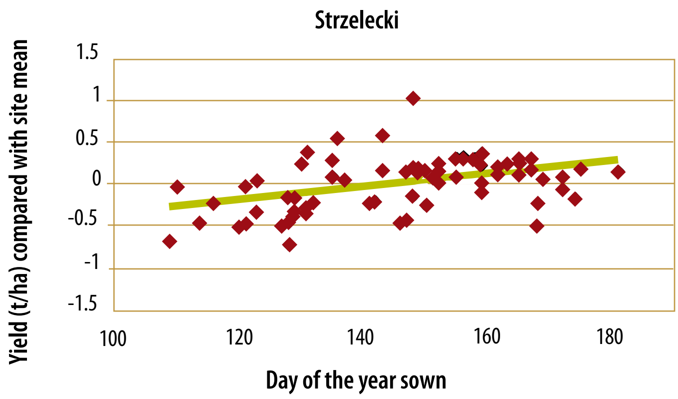
Source: 2007 Winter crop variety sowing guide, NSW DPI.



- **Wylah** is an example of a variety with stable yield across a wide range of sowing times. This response is shown by a horizontal trend line, with only small deviations from the line.



- **Whistler** has a higher relative yield from early sowings. This response is shown by a negatively sloping trend line.



- **Strzelecki** and **Ellison** are examples of varieties where the earlier the sowing time the lower the yield. This response is shown by a positively sloping trend line.

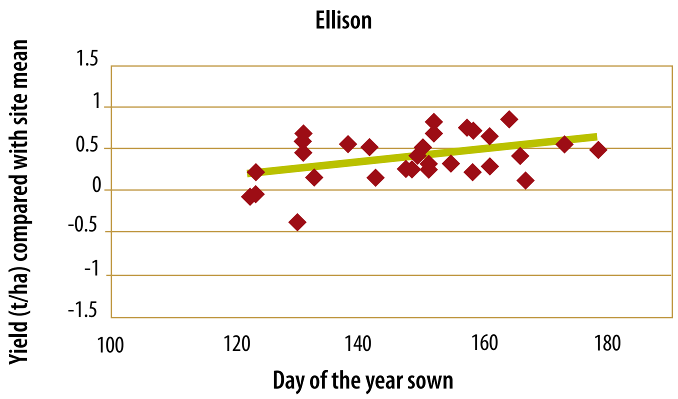


Figure 2–12: Yield responses of different varieties to sowing day. Variety response to sowing time is measured by grain yield (t/ha) relative to the site mean. The site mean is set to zero and graphed against the day of the year sown. 15 May = year day 135.
Source: Based on P Martin, C Lisle, A Milgate & S Brindle 2005, 'Time of sowing–effects and sources of information', presentation at Temora Field Day.

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IN THE PADDOCK

The following are some examples of what can be done in the paddock to demonstrate the stages of growth and development that have just been discussed. These are practical exercises to help farmers assess the progress of their crops at the vegetative stage.

Examining the root system

Aim: to check the root system of the crop for the presence of secondary roots and for signs of disease.

1. Carefully dig up 10 plants.
2. Wash soil away from the roots.
3. Find the primary root and determine whether there are secondary roots.
4. Look for the sub–crown internode.
5. Do the roots look healthy? Is there any sign of disease?
6. At flowering, excavate a hole around a plant and trace the root depth. How deep are the roots? Are there soil limitations to root growth?

Assessing plant growth stage

Aim: to accurately assess the current crop growth stage. Always assess the main stem.

1. Carefully dig up a plant.
2. Identify the main stem and the tillers. Turn the plant upside down and grab the longest leaf. This leaf is attached to the main stem. The main stem should also be the thickest. The other stems are the tillers.
3. Count the number of fully unfolded leaves on the main stem.
4. Count the number of tillers (if any).
5. Look closely at the oldest leaf and find the auricle and ligule.
6. Compare with Zadoks decimal code and record the growth stage in the table below.
7. Repeat this procedure with five plants and record the results.
8. Repeat this exercise with different varieties and different sowing dates.

GROWTH STAGE		
PLANT	PADDOCK 1	PADDOCK 2
1		
2		
3		
4		
5		

IN THE PADDOCK

Tiller counts

Aim: to assess the number of tillers/m² to compare different nitrogen rates, varieties or sowing rates.

1. Assess the crop when it is at Z30.
2. Count the number of tillers per plant along 0.5 m of row.
3. Do this at 10 locations within a paddock.
4. Add the 10 counts together and divide by 5 to give the average number of tillers/m of row.
5. Multiply the tiller counts by the row spacing factor to convert tillers/m of row to tillers/m^2

17.5 cm = 5.71	20 cm = 5.00	33 cm = 3.03
22.5 cm = 4.44	25 cm = 4.00	36 cm = 2.77
27.5 cm = 3.36	30 cm = 3.33	40 cm = 2.50

6. Repeat in a second paddock and record the results.

TILLERS		
COUNT	PADDOCK 1	PADDOCK 2
1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
Total		
Average per m row		
Tillers/m^2		

IN THE PADDOCK

Dry matter assessment

Aim: to determine what quantity of dry matter is available to graze. Assess the crop when its root system is firmly anchored.

1. Using a quadrat, cut a known area to ground level.

2. Repeat this process at five locations.

3. Mix all the samples together and weigh out a 150-g subsample. This is the wet weight.

4. Very carefully dry the subsample in a microwave. Place a cup of cold water in the microwave with the sample. Replace the water when it begins to boil.

5. Calculate the dry matter percentage by using the following formula:

$$\text{Dry matter \%} = \frac{\text{weight of dry sample (g)} \times 100}{\text{weight of wet sample (g)}}$$

6. The quadrat conversion factor is:
   a 30 cm × 50 cm quadrat = 0.15 m^2 or 1/66,666th ha, so × 67 to get kg DM/ha
   a 50 cm × 50 cm quadrat = 0.25 m^2 or 1/40,000th ha, so × 40 to get kg DM/ha.

HERBAGE MASS (kg DM/ha)			
CUT	WET WEIGHT	DRY MATTER %	HERBAGE MASS
1			
2			
3			
4			
5			
Average			

Monitoring for pests, diseases and injury

1. At regular intervals, walk a transect across the paddock.

2. Stop at five locations and check the plants for signs of insect damage or disease.

3. Look for nutrient deficiency symptoms and herbicide effects.

IN THE PADDOCK

Thermal time

Aim: to calculate the accumulated thermal time for a location.

1. Using the records from the nearest meterological station, calculate the mean temperature for each day.

$$\frac{\text{Daily maximum temperature + daily minimum temperature}}{2}$$

2. Add the mean temperatures together to give the accumulated degree-days.

DAY	MAXIMUM	MINIMUM	MEAN	ACCUMULATED DEGREE-DAYS
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
17				
18				
19				
20				
21				
22				
23				
24				
25				
26				
27				
28				
29				
30				
31				
TOTAL				

3. Reproductive development

by Jan Edwards & Karen Roberts

Chapter Snapshot

Introduction

The reproductive phase of the wheat plant continues the process of determining final yield. Vegetative growth prepared the plant to form the developing head and yield components. Management and environmental conditions during vegetative growth, and environmental stresses during the reproductive phase, determine the maximum yield that can be set by the plant within its genetic potential.

Knowledge of the stages of reproductive development helps farmers manage the plant during this phase to minimise the effects of various stresses and maximise yield.

Learning Outcomes

At the end of this chapter, you will be able to:

- recognise the change from vegetative growth to reproductive development
- identify stem elongation, floret formation and anthesis
- describe the effects of frost, heat and moisture on reproductive development
- understand the role of the decision-support tools Sowman® and Wheatman®
- determine the flowering window for a variety, taking into account location
- assess the growth stage of a crop, particularly for the purposes of nitrogen topdressing, herbicide application and removal of grazing stock.

Reproductive development Z14–Z69

Primordia
are organs in their earliest stage of development.

The reproductive phase begins when the shoot stops forming leaves and begins forming a head, a process known as head initiation. Within the head are the developing floral structures. This is a complex phase with a number of developments happening at the same time. (See *Introduction*, Figure iii, which shows the development stages of the wheat plant, including the overlap in reproductive development).

Head initiation (Z14)

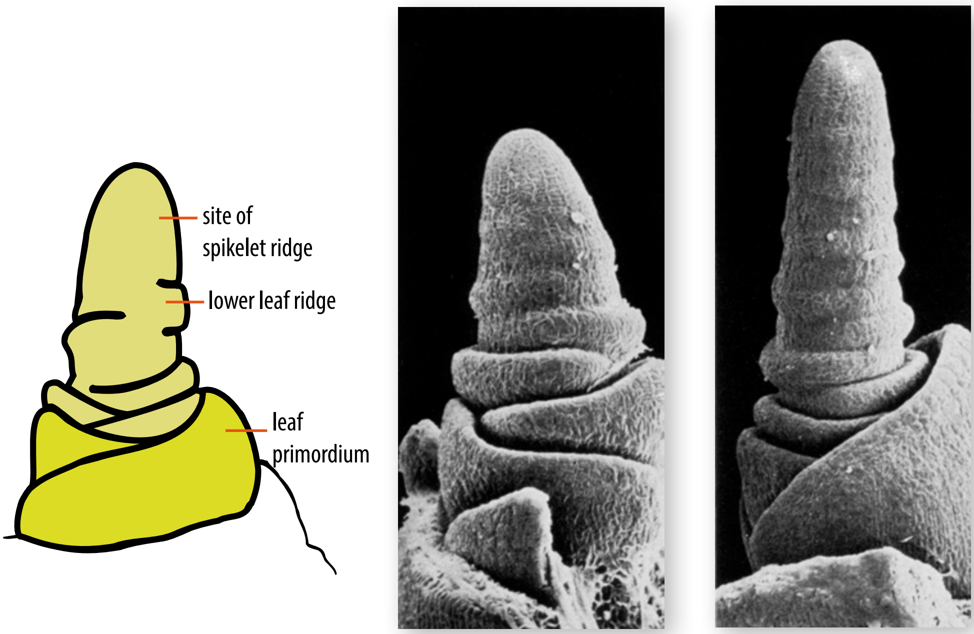
In the vegetative stage, the shoot apex produces leaves from single ridges until it begins to elongate or extend. The ridges then form too quickly to grow into leaves, so the cells reorganise to produce the head instead. This stage is called head initiation, and the plant now begins reproduction.

The elongation of the apex is not yet visible to the naked eye. Figure 3–1 shows the elongation of the apex with the beginnings of the ridges that develop into spikelets. The leaf **primordia** at the base still grow into leaves but those higher up are halted in early development and form spikelets instead.

Double ridging

During the double ridging stage a series of paired ridges or swellings develop on the elongating apex. The upper ridge swells and becomes the spikelet, while the lower leaf ridge stops developing and disappears. This stage can be seen under a microscope, as shown in Figure 3–2. At double ridging, the apex grows from 0.5 to 1.2 mm long.

Double ridging doesn't occur at a fixed vegetative stage but usually at around the time of the emergence of the fourth or fifth leaf, at about the start of tillering.



a. b. c.

Figure 3–1: a, b & c: The elongation of the apex, with the beginnings of the upper spikelet and lower leaf ridges.
Source: photos, CSIRO; illustration: E Kirkby & M Appleyard, 1984.

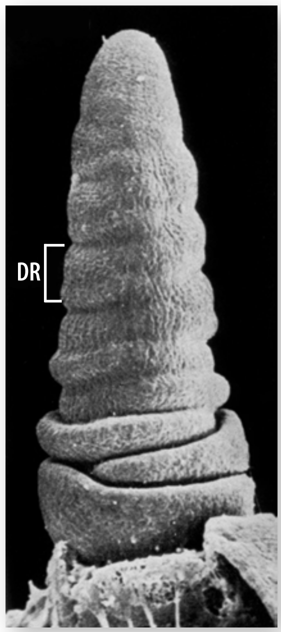


Figure 3–2: The changes in the elongating apex as the double ridges (DR) begin to form.
Source: CSIRO.

Spikelet initiation

The first spikelet ridges, which develop into the first spikelets, initiate in the centre of the apex and then form progressively towards either end of the head. This pattern of development continues into flowering and grain filling, so that the most advanced and mature components are in the centre of the head. This is why the middle section of the head at maturity has the most grains in the spikelet.

Spikelet initiation finishes when the apex produces a terminal spikelet (see page 54).

During this time the apex initiates around eight to 15 leaves, depending on variety and time of sowing, before it initiates the spikelets. In spring wheats, spikelets are initiated at a constant rate of 0.5 to 1.5 per day or 9 degree-days per spikelet. In winter wheats, initiation of spikelets occurs throughout the winter, slowing during cold spells.

By the end of the phase all the spikelets on the head that will eventually set grain are more or less the same size and at the same stage of development.

The potential number of spikelets per head is higher with a long vegetative stage. The length of this stage is determined by genetics, such as whether it is a spring or winter wheat, not the sowing date. However, the actual number of spikelets is determined by the length of the reproductive phase. Short days (8 hours) from double ridging to terminal spikelet stimulate a large number of spikelets. Table 3–1 shows approximately how many degree-days it takes to reach each development phase.

At the same time as the head is developing, the initiation and growth of the tillers is taking place.

Development of the head within the tiller takes place in the same way as that of the main shoot. Tillering is usually complete by the end of the terminal spikelet stage, so the potential size of two yield components has already been set: the number of heads and spikelets.

All the events up until now have occurred while the shoot apex is completely enclosed in the developing leaves and is at, or just below, soil level.

By the end of the terminal spikelet stage, the potential size of two yield components, the number of heads and the number of spikelets, has been set.

Table 3–1: The approximate duration of critical development stages in cumulative degree-days (°C).

MATURITY GROUP	EMERGENCE	DOUBLE RIDGE	TERMINAL SPIKELET	ANTHESIS	PHYSIOLOGICAL MATURITY
Late	166 (12)	770 (61)	921 (75)	1488 (119)	2530 (161)
Medium	166 (12)	628 (48)	774 (62)	1386 (111)	2415 (154)
Early	166 (12)	482 (36)	682 (52)	1286 (106)	2296 (148)

Days after sowing are shown in parenthese. The data are based on the mean of the varieties.

Source: M Karini & K Siddique, 1991.

Floret formation

The floret contains the reproductive parts of the plant. Floret formation begins part way through spikelet initiation (see Figure 3–3). The spikelet ridge forms the spikelet containing several florets and the two glumes. The glumes are strong protective structures on the outside of the spikelet and are the first two structures seen. The lemmae then form inside the glumes. Eventually the florets are enclosed by the lemma on the outside and the palea on the inside. Once enclosed, the floral structures start forming. Each floret develops two lodicules, three stamens and a carpel.

As the spikelets grow, the florets form on opposite sides of the spikelet stem (rachilla). The first florets develop within spikelets on the lower to central part of the developing head. The central spikelet can initiate up to 10 florets. Spikelets towards the tip and base initiate fewer florets (six to eight). Less than half these florets complete anthesis resulting in three to six potentially fertile florets per spikelet, only the fertile florets setting grain. The rest abort or are immature at fertilisation. In a typical wheat crop, only 30% to 40% of florets set grain.

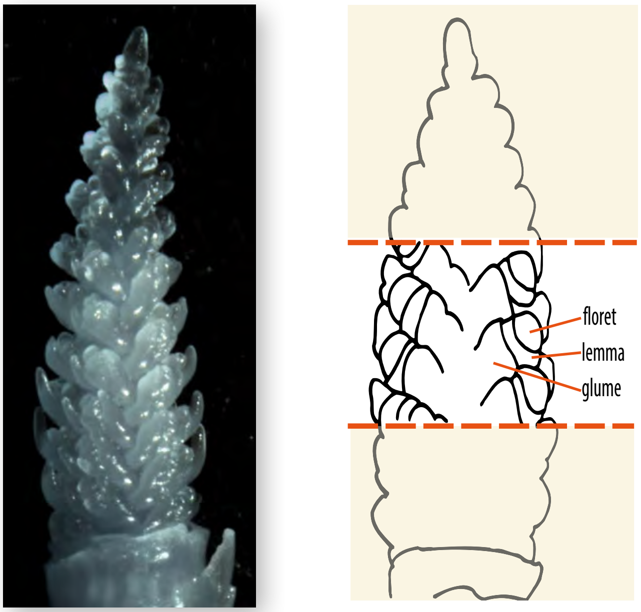


Figure 3–3: The initiation of the spikelet and florets. The most advanced spikelets are in the mid part of the apex.
Source: photo, CSIRO; illustration, E Kirby & M Appleyard, 1984.

Terminal spikelet

When the wheat head nears completion, the apex initiates the terminal spikelet (Figure 3–4). By the end of this stage, no more spikelets are initiated, the number set varying between 20 and 30. Within each of the spikelets, several florets continue to initiate and develop their floral parts. After the terminal spikelet is initiated, rapid growth of the head begins and the stem elongates.

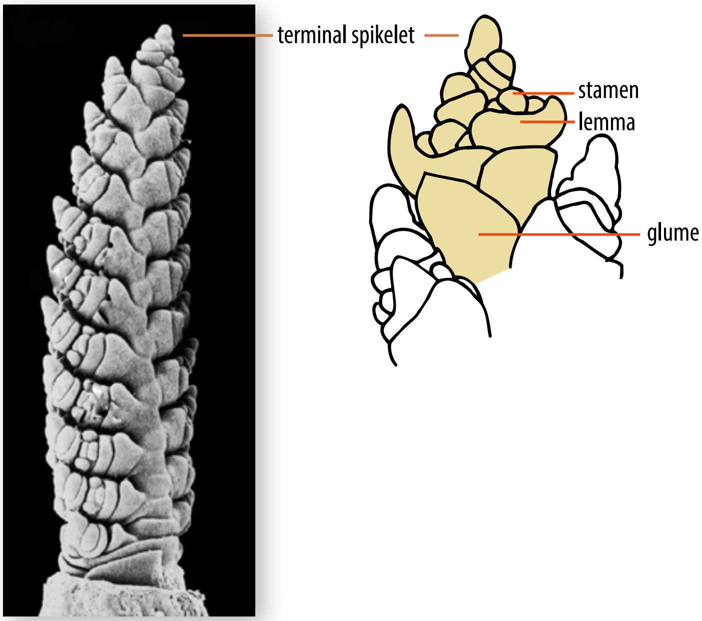


Figure 3–4: The structure of the head at the terminal spikelet stage with illustration showing the terminal spikelet. The apex is about 4 mm long and is just above the soil surface.
Source: photo, CSIRO; illustration, E Kirby & M Appleyard, 1984.

Head at 1 cm (Z30)

The developing head is not visible until it is at least 1 cm above the ground. Once the terminal spikelet is formed, stem elongation begins. Rapid stem growth brings the well-developed head from below ground to above ground.

Head at 1 cm (Z30) is a key development stage for the end of grazing. Because the terminal spikelet can't be detected in the field or related to a specific Zadoks code, head at 1 cm is a commonly accepted indicator stage for terminal spikelet and associated management decisions.

Because head at 1 cm can be detected in the field with dissection (see Figure 3–5), it is a useful indicator for the removal of grazing animals, the application of nitrogen, and the limit for application of many herbicides. (See *Herbicides* on page 63).

Stem elongation (Z31–Z36)

Stem growth is the result of the elongation of the internodes. The crown consists of eight to 14 nodes stacked closely above one another, separated by internodes less than 1 mm long. The growth of the first five or six internodes pushes the head higher and elongates the stem. Lower internodes remain compressed at the base, with the number depending on sowing rate and variety. When the internodes elongate the individual nodes become detectable.

Stem elongation occurs in an ordered sequence. An internode begins to elongate when the leaf associated with it reaches full size. When this internode is half its final length the one above it begins to grow, and this continues until the last internode (the peduncle, which carries the head) is fully elongated and the stem is at its final length. Each internode is longer than the last, so that the peduncle is the longest of all.

Above the node is the swollen leaf base (see Figure 3–6) which has an important role if lodging occurs. If the crop is laid flat, the stems turn upwards and, in response to gravity, the side nearest to the ground grows at a faster rate than the side facing upwards. This causes the swollen leaf base to become uneven, turning the stem and head upwards. It may take two or three leaf bases to bring the peduncle upright.

Figure 3–5: The beginning of stem elongation can be seen by slicing the main tiller with a sharp blade to expose the head. The plant shown is at the stage 'head at 1 cm'. The length is measured from the tiller and root insertion point to the tip of the young head.
Photo: J Wilkins.

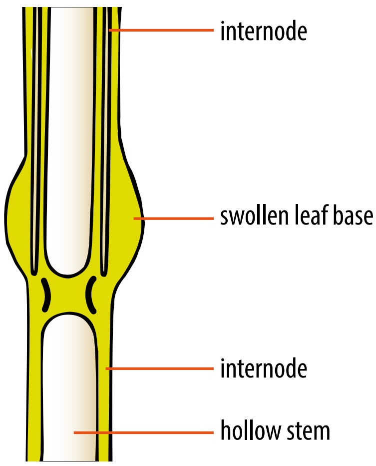


Figure 3–6: Cross-section and photo of the stem, showing the node and the swollen leaf base that can be felt as a hard lump.
Source: Illustration, E Kirkby & M Appleyard, 1984; photo, L Turton.

Internode
the tissue between two nodes that elongates, producing stem growth.

Nodes
are where parts of the plant such as leaves, tillers and spikelets join the plant.

Ear peep
is when the terminal spikelet of the head is visible.

Carpel
is the female part of the flower; consists of the ovary, styles and three stigmas.

The swollen leaf base can be felt as a hard lump when feeling along the stem. The first node can then be located and used as an indicator of the position of the head in the stem for determining when to remove stock.

Stem elongation is a time of intense competition for nutrients and moisture. The developing parts are sensitive to environmental stress, in particular deficiencies in moisture and nitrogen. If stress occurs, the secondary and weak primary tillers of the plant abort, while the main stem and the stronger primary tillers continue to grow. This is an example of the wheat plant's ability to adjust to environmental conditions. The plant stops the growth of the weaker tillers to ensure it has the resources to properly fill the grain in the primary tillers. The result is tiller death and fewer heads/m^2, but the grain that is produced is filled properly. (See *Factors affecting reproductive development* on page 58).

At this time the head also begins to grow in size. Growth is slow in the early stages and increases greatly when the ligule (the join between the leaf blade and the sheath) of the flag leaf becomes visible (Z39).

Flag leaf extension (Z39)

The flag leaf is the last leaf to develop and is located just below the head. At this stage, the plant is about 40 cm tall. The flag leaf is fully emerged when the ligule becomes visible between the blade and sheath.

It takes an average of 25 days from this point to reach mid-flowering (Z65). The duration drops to 20 days for hot periods and increases to 30 days for cool periods. 'Ear peep' occurs half way through this period.

The emergence of the flag leaf is a key indicator for application of fungicides. It needs to be protected because it is the most important leaf for photosynthesis and gathering energy for grain fill. The flag leaf contributes around 43% of the carbohydrate for yield. (See *Chapter 4: Grain development*, *Contribution of plant parts*).

The emergence of the tips of the awns (awn peep, see Figure 3–7) is an indicator that the flag leaf is fully extended (Z39). Awns are extensions of the tip of the lemma. As part of the head, they contribute to photosynthesis.

Booting and head emergence (Z41—Z60)

Booting is the swelling of the head within the 'boot' formed by the sheath of the fully extended flag leaf (Figure 3–8). The position of the head or boot in relation to the ligule of the second leaf determines the boot stage.

Figure 3–7: Awn peep.
Photo: J White.

Figure 3–8: The head is emerging from the boot.
Photo: L Turton.

The boot opens and the first awns are visible (Z49). The head has reached its full length when the tips of the awns emerge from the tip of the flag leaf sheath.

The terminal spikelet of the head becomes visible (ear peep, Z51), and emergence continues until the head is completely emerged (Z60). At this stage, the yellow anthers are still within the florets.

Floret development

This phase extends from the terminal spikelet stage, when the lower florets in each spikelet have all the floral parts present, until shortly after head emergence when the stamens and carpel are fully mature and anthesis takes place.

There are three stages of floret development: the white, green and yellow anther stages. These are important to identify, because they indicate the fertility of each floret and whether a grain will be set. The three colours can be seen in the paddock when the floral structures are pulled apart.

White anther stage

The anthers begin as a creamy translucent white. The stamens are very short, and the anthers have four lobes. The carpel is very small and has hornlike outgrowths that become the styles.

Green anther stage

In the green anther stage, the carpel grows rapidly and develops styles and the start of feathery stigmas. The anthers are bright green, have short filaments and are around 1 mm long (Figure 3–9). No more florets are initiated. Reproductive cell division (meiosis) occurs in the anthers and carpel during the green anther stage, coinciding with booting. This stage is very sensitive to moisture, frost and heat stress. Stress at this point results in reduced floret numbers.

Figure 3–9: Green anther stage.
Photo: L Turton.

Figure 3–10: A mature floret in the yellow anther stage. The stigmas are receptive to pollen and the yellow anthers are about to release pollen.
Photo: CSIRO.

Yellow anther stage

In the yellow anther stage, the surviving florets are mature and anthesis is about to take place (Figure 3–10). The anthers swell and change colour from bright green through pale green to bright yellow. The changes in colour relate to pollen ripening. The youngest florets towards the tip of the spikelet abort at this stage.

Anthesis (Z61—Z69)

Anthesis (flowering) is the bursting of the pollen sacs and fertilisation of the carpel. Florets self pollinate in 96% of cases. After fertilisation the empty anthers appear on the outside of the head (Figure 3–11).

Anthesis is a short phase lasting only a few minutes in an individual floret, a couple of hours in a head and about three to four days across a dryland crop. The process usually begins as the temperature rises, often at dawn, though it may happen later in the day depending on temperature and humidity. The end of anthesis is marked

Figure 3–11: Anthesis is over and the empty anthers dangle from the spikelets.
Photo: J Edwards .

by the extrusion of anthers (Z65), which usually takes 12 to 24 hours, provided moisture is not limiting.

There can be several days or weeks between the initiation of the first and last spikelet. Despite developing at different rates, the spikelets on each head flower together. In fertile florets, flowering begins in the central part of the head, extending up and down the head. In the central spikelet, the outer florets are fertilised slightly earlier than the inner florets and are heavier in weight. However, all the grains grow and ripen together.

Factors affecting reproductive development

Environmental stress has the greatest impact on yield from first spikelet initiation to anthesis, as spikelet and floret numbers are established during these phases. Floret survival is greatest where environmental stress is low with adequate water and nutrient supplies, optimum temperatures, and high solar radiation.

Final grain yield is largely determined by grain number, which is set by floret production and survival. There is a critical period 2 to 3 weeks before anthesis when water stress and/or high temperature may greatly reduce floret production and survival, significantly reducing grain number per spikelet.

Moisture stress

Rapid growth is taking place during the reproductive phase and the plant draws heavily on available moisture. When water supply from the roots is slowed the leaves become stressed, heat up and stop photosynthesising. This reduces the amount of resources the plant is generating and has a direct impact on yield.

Head growth

There is a significant decrease in grain number when moisture stress occurs during head growth. Yield reduction is greatest when moisture stress occurs 10 days before head emergence (Z59). During this stage stress decreases the number of spikelets and causes the death of the florets at the tip and base of the head.

Drought causes large reductions in yield by decreasing grain number/m^2 (not grain weight). Drought advances the flowering time of all varieties. The plant compensates for limited resources by hurrying to flower and set grain before resources are exhausted.

Anthesis

The 10 days either side of anthesis are critical to final yield, because during this period the plant will only set the number of grains it has the resources to fill. So a good water supply and a high leaf area index are essential to provide sufficient resources for the plant to set a high number of grains.

Moisture stress close to anthesis reduces the accumulation of water-soluble carbohydrates in the stem, meaning there are fewer stored carbohydrates to transfer to the developing grain during grain fill. Rainfall just prior to anthesis will not undo the damage to potential yield from previous moisture stress.

Pollen is also highly vulnerable to water deficit at formation. Stress at this stage causes sterility because of an insufficient supply of carbohydrates.

Temperature

During reproductive development, temperature extremes beyond the optimum range of 5° to 28°C affect development, photosynthesis and the reproductive parts. Matching the anthesis date to the least stressful period is a way to minimise yield loss from frost or high temperatures. The aim is to have all crops flowering in their optimum window, and this is why varieties with different

Table 3–2: Response of phasic development to temperature, photoperiod and vernalisation.

DEVELOPMENT PHASE	TEMPERATURE	PHOTOPERIOD	VERNALISATION
Sowing – emergence	★★★★/★★★★★	0	0
Emergence – double ridge	★★★/★★★★	0/★★★	0/★★★★★
Double ridge – terminal spikelet	★/★★★	0/★★★★★	0/★★★★★
Terminal spikelet – heading	★★★/★★★★★	0/★★★	0/★(?)
Heading – anthesis	★★★/★★★★★	0/★(?)	0
Anthesis – maturity	★★★/★★★★★	0	0

Source: Based on G Slafer & H Rawson, 1994.

maturities need to be sown at different times. However, there is always a trade-off in yield with some loss due to heat and frost, and extreme conditions may still occur in the flowering window. (See *Flowering Time* on page 60).

Table 3–2 is an estimation of the sensitivity of wheat to temperature stress at various growth stages. An arbitrary scale is used to show when the effects are strong (★★★★★), moderate (★★★) or slight (★). 0 denotes that the factor does not affect the process and (?) refers to uncertainty in the literature. Genetic variation in response was considered for each factor.

Heat stress

High temperatures are common during flowering and grain fill, and are usually accompanied by moisture stress. Heat stress at this time has a large impact on grain yield through a reduction in the potential number of grains.

As the temperature increases, the plant pulls in more water from the soil and evaporates it from the stomata in the leaves in an attempt to cool itself (transpiration). If the temperature becomes very high, transpiration becomes so rapid that more water is lost than is taken up by the roots. The plant then closes its stomata to prevent wilting and reduce water loss. This decreases photosynthesis and transpiration, causing leaf temperature to once again rise. Leaf photosynthesis declines as temperatures exceed 35°C, and at 45°C photosynthesis is halved.

When the plant shuts down in this way, it reduces the flow of carbohydrates and other resources to the developing plant parts. Rapidly dividing cells, such as those in reproductive plant parts, need an uninterrupted supply of resources to prevent damage.

Pollen sterility and flower abortions are also common results of heat stress. Temperatures above 30°C during floret formation cause complete sterility. During the 30 days before anthesis, the number of grains decreases by 4% for each degree increase in mean temperature above 14°C. There are fewer fertile heads or fewer grains per head.

Cold and freezing

Frost damage can occur at all stages of crop development but is particularly damaging between flag leaf emergence and 10 days after anthesis. Frost damage is usually very patchy and is influenced by factors such as temperature, soil type and colour, soil moisture, cloud cover, wind speed, topography, crop species, crop nutrition and crop density.

Damage usually occurs when tissue temperatures reach approximately –3.5°C on calm, clear nights. Damage increases as temperatures fall below this level. Damage also increases when plants are moisture stressed.

There is currently no genetic resistance to frost, although some species are more susceptible than others. Research

Frost damage.
Photo: J Edwards.

in New South Wales and Queensland suggests that the critical crop temperature for yield loss in wheat is about –3.8°C.

Crop temperatures need to fall to –4°C or below to freeze stems or heads during stem elongation and booting. Partial freezing of the stem and developing head distorts their growth in a similar way to hormonal herbicides, nutrient deficiency, disease or moisture stress. Frost-affected stems, displaying a ring of white tissue where the sap has frozen, or blistering and cracking, restrict movement of resources to the developing head. Occasionally the head can get frosted in the stem, resulting in part or all of the head emerging white.

After head emergence and at flowering, the sensitive reproductive structures are directly exposed to the surrounding air, making them particularly vulnerable to frost damage. Damage is not always visible; often the reproductive parts that look unaffected will not produce grain.

Frost damage causes complete or part sterility of the anthers. The damage appears as aborted spikelets anywhere in the head (unlike moisture stress, when spikelets are aborted from the tip and base of the head).

It can also cause sterility of florets in parts of the entire spike. The florets are bleached, shrivelled or dwarfed. Because flowering starts in the middle of the head, progressing towards the top and bottom over a few days, there can be considerable variation in the effect on the grain, depending on the stage of development of the floret at the time of the frost. The damage to the florets results in less grain being set.

Damage after flowering usually results in pinched grain.

Flowering time

It is critical to match variety and sowing date so that flowering occurs early enough to allow a long grain-filling period before the high evaporative demands and soil water deficit of early summer. The flowering period must also be late enough to avoid damage by frosts in early spring (Figure 3–12). Balanced with this is the need for a vegetative period long enough to support crop growth and the production of fertile florets, both of which determine yield potential.

Trials in northern New South Wales calculated a reduction in relative grain yield of 9% to 13.5% for each week that flowering was delayed after the first week of October.

To determine the optimum flowering time it is important to know the frost and heat risk for your area. Table 3–3 lists the frost risk at different locations in New South Wales. It also shows the heat risk. In the table, 0°C has been used to simulate a severe frost and 2°C to simulate a mild frost. (See also *Chapter 2: Vegetative growth, Plant maturity*).

The data are based on long-term weather records, but the risk of frost or heat stress varies from season to season.

Sowman® and Wheatman® are two decision support computer programs that combine meteorological data and phenological field data to help determine the most appropriate sowing time for varieties on the basis of risk of frost and heat damage. The NSW Department of Primary Industries' *Winter crop variety sowing guide* also provides a more generalised sowing window for different varieties, based on the same data.

Table 3–3: Approximate dates for frost risk at different locations in New South Wales.

SITE	0°C IN THE SCREEN 10% CHANCE OF SEVERE FROST	2°C IN THE SCREEN 10% CHANCE OF MILD FROST	DATE WHERE 10% CHANCE > 30°C
Moree	17 August	7 September	21 September
Dubbo	22 August	17 September	11 October
Cowra	25 August	11 October	27 October
West Wyalong	17 August	17 September	17 October
Hay	19 July	27 August	8 October

In the screen *is the temperature as measured at the meterological station, 1.3m above ground.*

Source: Analysis of SILO data 1900 to 2006.

- Maximum yield is achieved when there is minimal exposure to frost or the high temperatures and moisture deficit of summer.

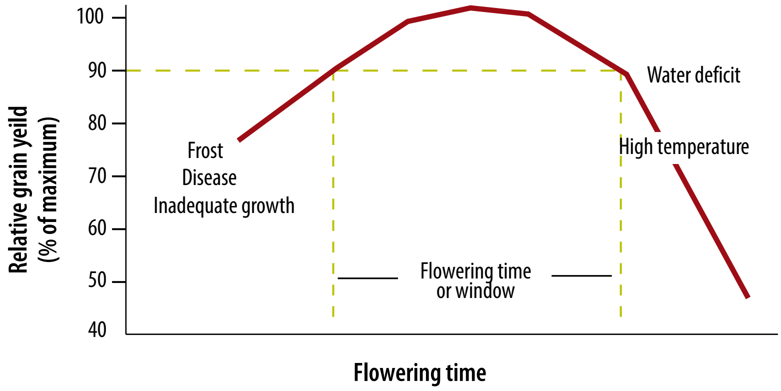


Figure 3–12: The flowering window. The optimum flowering time depends on location and the acceptable frost risk.
Source: Based on W Anderson & J Garlinge, 2000.

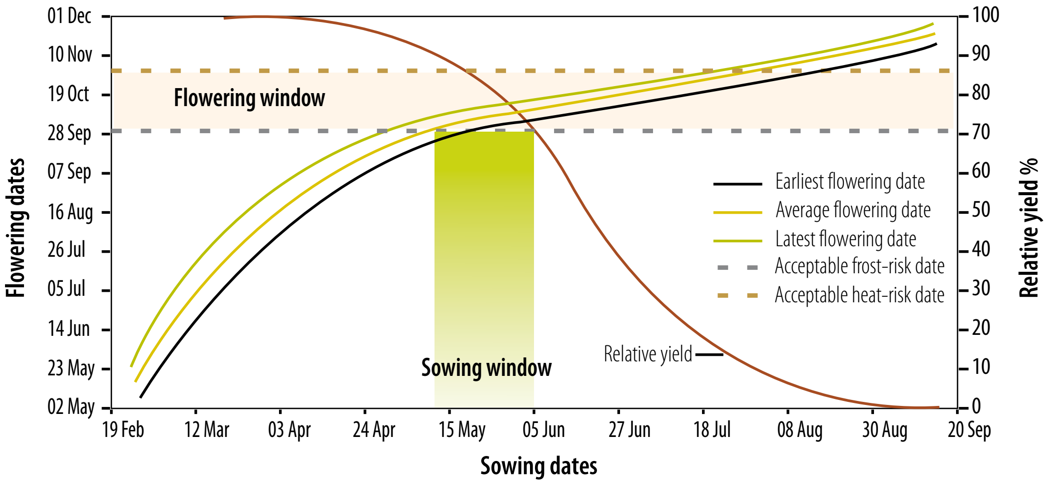


Figure 3–13: Sowing and flowering window for the variety Ellison at Cowra.
Source: Sowman, decision support system.

- The sowing and flowering windows are calculated on the basis of acceptable frost and heat risk.

- Location changes the number of days to anthesis.
- The graph shows the response of Janz when sown in May at different locations in NSW.
- The variety is much quicker to flower in northern NSW than southern.

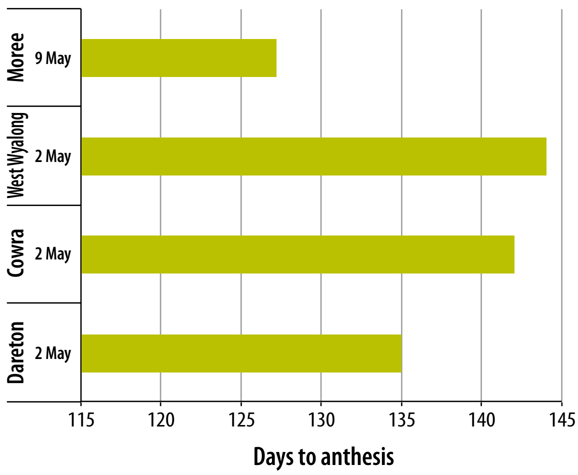


Figure 3–14: Days to anthesis of the variety Janz, sown in May 2006 at various locations in New South Wales.
Source: NSW Department of Primary Industries, phenology trials.

Figure 3–13 shows the estimated flowering window for the variety Ellison at Cowra. The Sowman model has been run with an acceptable heat and frost risk of 1 year in 7. It has also been run to accept a potential yield of 70% or better on the basis of rainfall data for the site. Sowman estimates the flowering window to be between 28 September and 5 November.

It also needs to be taken into consideration that the time it takes a variety to reach maturity varies depending on where it is being grown and the season. This is demonstrated in Figure 3–14, which shows the days to anthesis with the variety Janz, sown from April to May at a number of locations across New South Wales.

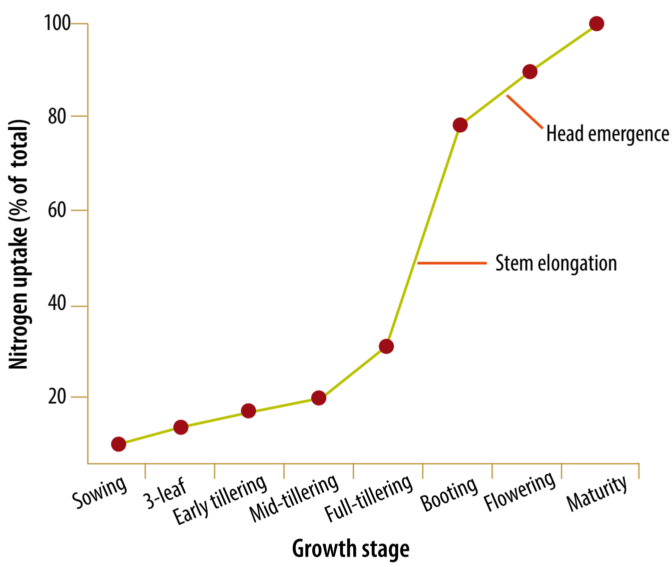


Figure 3–15: Relationship between growth stage and accumulated uptake of nitrogen by a wheat crop, expressed as a percentage of the total uptake.
Source: Based on N Fettell, 2006, 'Crop growth, yield formation and management.' NSW Department of Primary Industries, District Agronomists technical update papers.

- 60% of total nitrogen is taken up during stem elongation and head emergence.

Nitrogen

Demand for nitrogen is greatest during stem elongation and head emergence. This is a period of rapid dry matter production during which 60% of total nitrogen uptake occurs (see Figure 3–15). The nitrogen concentration in the head at anthesis relates closely to grain number and therefore yield.

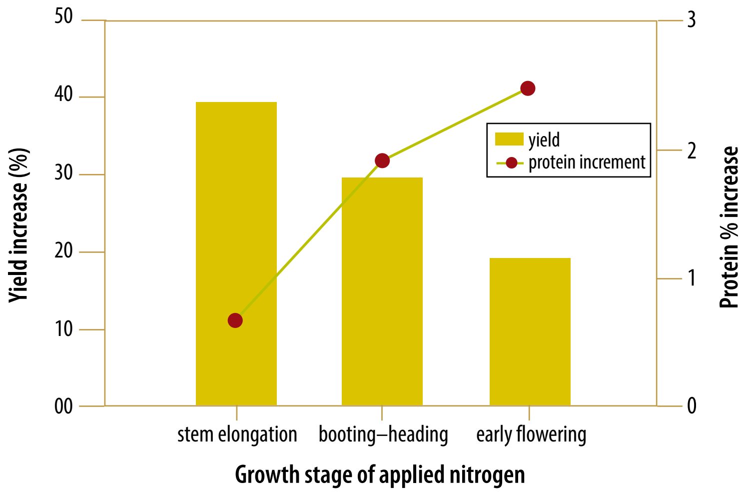
Because of the cost and potential economic risks associated with nitrogen topdressing it is best to carefully assess the agronomic state of the crop and its yield potential before applying nitrogen. Do not apply nitrogen to crops suffering waterlogging, disease (foliar or root) or weed competition, as the crop will not respond to increased nitrogen and applied nitrogen may be lost. It is also essential to assess how much nitrogen is presently available to the crop.

The difficulty of predicting rainfall events makes topdressing nitrogen as granular fertiliser (urea) risky in northern New South Wales. Split applications are more common in central and southern New South Wales.

For efficient recovery of urea nitrogen, moisture needs to move from the surface into the topsoil, carrying the nitrogen into the profile, where it makes contact with actively growing roots. A rainfall event of 5 mm or more is required soon after application.

As a general rule, applications of nitrogen from sowing to stem elongation increase yield, while applications after stem elongation increase protein (Figure 3–16). The later nitrogen is applied, the less time there is for it to be moved into the root uptake zone to be available to the plant.

- Nitrogen applied during early tillering (Z23–Z29) has the greatest impact on yield by increasing or maintaining tillers. Nitrogen applied at this stage is used almost as efficiently as that applied at pre-sowing. About 40% to 50% of the applied nitrogen is used by the plant.
- The application of nitrogen at stem elongation (Z30–Z40) increases yield by maintaining existing tillers and also slightly increases protein in the grain (up to 1%). About 30% of the applied nitrogen is used by the plant.
- The application of nitrogen at head emergence (Z51–Z59) has the maximum effect on grain protein. About 20% of the applied nitrogen is used by the plant.



- 60% of total nitrogen is taken up during stem elongation and head emergence.

Figure 3–16: Effect of applying 100 kg N/ha (as urea) at various growth stages on yield and protein of commercial wheat crops in 1993. Source: Based on B Manning et al., 1998.

Herbicides

Herbicides are commonly used for weed control. All herbicides can cause problems for crops if applied incorrectly. Certain hormone-based herbicides need to be applied at the correct time to avoid damage to the developing head and subsequent yield loss. Herbicides are grouped according to their mode of action, and most of the hormone herbicides belong to Group I. These are also often called *phenoxy* herbicides.

Hormonal herbicides function in a similar way to plant growth regulators. The herbicides interfere with a number of biological processes and protein synthesis, causing growth abnormalities. They move quickly to areas of new plant growth, where they stop cell division. In particular, they can stop pollen cells dividing and significantly reduce pollination of the crop.

Hormonal herbicides also cause leaf distortion and rolling, reduced tiller number, sterility of florets or spikelets, abnormal head emergence, stunting and delayed heading, all of which affect yield.

Hormone herbicides are those that contain the following active ingredients: MCPA; MCPB; 2, 4–D; 2,4–DB; dicamba; picloram; triclopyr; clopyralid; or combinations of these and other herbicides.

When applying any chemical, in particular these hormone herbicides, it is important to carefully observe the crop's growth stage, adhere to the recommendations on the label, and time the spray correctly. The time taken for the crop to change from being safe to apply herbicide to unsafe can be as short as 6 days. Applying these herbicides under moisture stress may contribute to a reduction in yield.

There are usually three key stages to consider when timing herbicides to avoid damage to reproductive parts. These are:

- double ridging, which occurs around the fourth to fifth leaf stage (Z14–Z15)

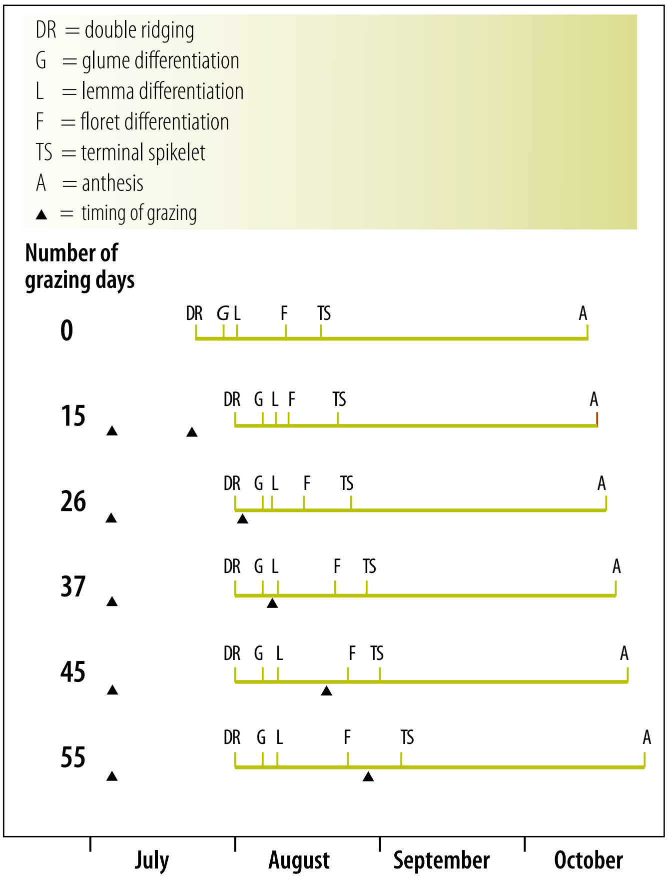


Figure 3–17: Grazing and development of wheat, Cookardinia 2004
Source: Based on J Virgona, F Gummer & J Angus, 2006.

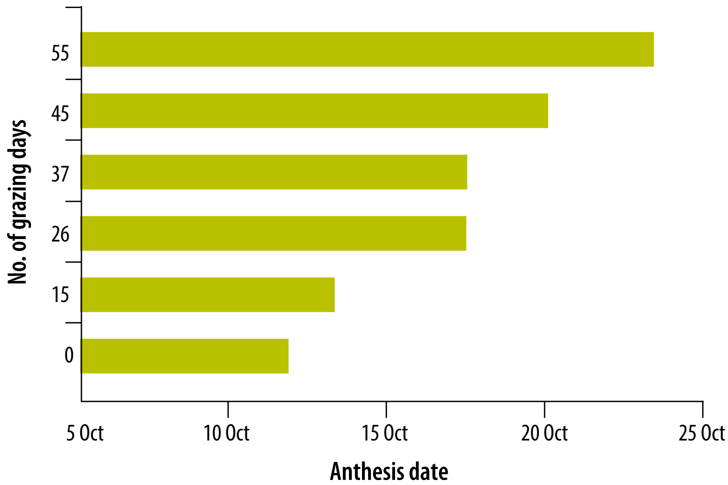
- Grazing alters the timing of stages of development in wheat crops.

- stem elongation, which is also when the head is at 1 cm and the terminal spikelet has been formed. This indicates the end of tillering and the start of the reproductive phase (Z30)
- pollen formation, a particularly sensitive stage that usually occurs when the flag leaf is fully emerged at Z39, around 10 to 12 days before head emergence. The cut-off for 2,4–D and MCPA is when the flag leaf is just visible (Z37). Depending on the herbicide, it's too late when the awns are visible (Z51).

Detailed information on the timing of herbicide applications by crop growth stage can be found in the NSW Department of Primary Industries' annual publication, *Weed control in winter crops.*

Grazing

It is important to be able to accurately assess crop growth stage when grazing so that stock can be removed before the developing head is eaten. Because of the variation of development in the paddock,



- There is a significant delay in anthesis with high intensity grazing (55 days).

Figure 3–18: Impact of grazing on development at Cookardinia 2004.
Source: Based on J Virgona, F Gummer & J Angus, 2006.

always assess the main tillers that can be identified by the longest leaf. If grazing is continued beyond Z29 (when the first node can be felt and the head starts moving up the stem) and heads are eaten they will not regrow. With adequate moisture other tiller buds may develop into tillers and form heads. However, because of the delay in development, flowering is likely to be pushed into a period of high temperatures and low moisture. (See *Chapter 2: Vegetative growth, In the paddock*).

There are significant delays in flowering under high-intensity grazing. Research work carried out in southern New South Wales subjected the variety EGA_ Wedgetail to five different grazing treatments: ungrazed, 15, 26, 37, 45 and 55 grazing days. The results are presented in Figure 3–17 and Figure 3–18 and show the impact of grazing on development. Figure 3–19 shows the difference in development of the head.

Delay in flowering dates was also compared at two locations, Cookardinia and Wallendbeen, in 2004 and 2005 with different grazing intensity. The trend in delay occurred at both sites and was not due to stock eating the developing heads. The grazing of developing heads was

Figure 3–19: Delay in development of the head under different grazing intensities. Photo: K Condon.

measured and was minor in both years of the trial: less than 8% in 2004 and 3% in 2005.

The grazing delay can be seen by dissecting the plants. Figure 3–20 shows the difference in apical development of the wheat head under different grazing regimes. Where there was no grazing, the head is at a more advanced stage of development than with the other treatments, especially when compared with the most intense grazing.

The exact reason for the delay in development is not known. Grazing is known to alter the temperature in the canopy. Work carried out in 2006 at Charles Sturt University showed that grazed crops had lower apex temperatures at night than ungrazed crops. However, they also had much higher apex temperatures during the day. So changes in apex temperature don't explain the delay in development. Further investigations are under way.

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IN THE PADDOCK

The following are some examples of activities that can be done in the paddock to demonstrate the physiology discussed in this section. These are practical exercises to help farmers assess the progress of their crops at this stage.

Identifying Z30

Aim: to accurately identify Z30.

1. Carefully dig up a plant and identify the main stem and the tillers.
2. Remove the leaves on the stem.
3. Gently peel back the layers from the stem. This will expose the shoot apex.
4. Examine the head under the microscope and look at the components.
5. Dissect and examine a range of stages, particularly head at 1 cm.
6. Try to observe spikelets and other parts of the head when it is very small.
7. Demonstrate or compare the effects on a crop where the stock have been pulled out too late. What has happened to the head?
8. Compare plants at different growth stages. For example, compare a plant that is not yet jointing and the head is still below the crown with a plant where the head has elongated up the main tiller.
9. Discuss the impact of timing of stock removal on yield.

Nitrogen topdressing

Aim: to assess tiller number to determine if a topdressing response is likely. The tiller count is done at Z30 so there will be no subsequent mortality. The following is based on work by John Angus, CSIRO, NSW Department of Primary Industries and Incitec Pty Ltd, from 1987 to 1990.

1. Count the number of tillers per m^2 (see *Chapter 2 Vegetative growth: In the paddock, Tiller counts*), which gives an indication of potential yield (100 tillers/m^2=1 t/ha). No single test is as closely correlated with yield response as tiller number.
2. The following are some rules of thumb to explain the response to applying 40 to 50 kg N/ha. The rules apply where this is no disease or other nutrient deficiency and for crops sown before mid-June. For an average season in 400 to 600 mm rainfall zone in southern New South Wales:
   - less than 500 shoots per m^2, yield response positive, no effect on protein
   - 500 to 700 shoots per m^2, yield response unlikely, protein response positive
   - more than 700 shoots per m^2, yield response negative (due to likely haying-off), protein response highly positive.
3. Determine the impact of topdressing at each growth stage.
4. Determine the weather conditions required for topdressing.

IN THE PADDOCK

Flowering

Aim: to assess the stages of anthesis.

1. Dissect a head into spikelets and florets and identify the reproductive parts.
2. Look at a number of stages to try to see the differences in reproductive development, such as the different anther colours.
3. Identify frosted heads, anthers, stigmas and ovaries. Compare frosted to healthy parts.
4. Identify parts of the paddock that may have advanced/delayed flowering, or different topography etc. that make those patches more susceptible to frost.
5. Once identified, discuss options like sowing time, variety, species and other agronomic factors.

Modelling flowering time

Aim: to use decision support systems to predict flowering date.

1. Run through a Sowman® scenario.
2. Show how the different frost and temperature risks affect the flowering window.
3. Show selection of variety and sowing time to match the window.

4. Grain development

by Bill Manning, Klara Schulze & Tim McNee

Chapter Snapshot

Introduction

Chapter 4 explains how the grain develops and reaches physiological maturity, and the environmental conditions that influence its progression.

Grain development is the period from flowering to physiological maturity and is the final stage in the life cycle of the wheat plant. Carbohydrates and protein are deposited in the grain as it grows and ripens.

Final grain yield is determined during this phase and is influenced not only by current conditions and management decisions, but by everything that has preceded it. Grain **quality** *is greatly affected by the conditions during grain development.*

Learning Outcomes

At the end of this chapter, you will be able to:

- describe the stages of grain development
- list the sources of carbohydrate and protein for grain fill
- understand the impact of conditions during grain development on grain yield and quality
- identify the different components of yield, when they are set, and what influences final yield
- understand the principles of canopy management
- assess variations in grain size in the head
- estimate grain yield
- calculate harvest index and water-use efficiency.

Early grain enlargement.
Photo: L Turton.

Grain enlargement; the grain is still green.
Photo: M Dignand.

Dough development; the grain has turned golden.
Photo: M Dignand.

Grain development Z71–Z90

Grain development is the period from flowering to physiological maturity when fertilised florets fill and ripen to form grain. The wheat grain has three growth stages: grain enlargement, grain fill and physiological maturity (Figure 4–1).

Stage 1 Grain enlargement (Z71)

Grain enlargement begins after floret fertilisation and continues for 10 to 14 days or 180 degree-days. In the first 4 days after flowering, the seed increases rapidly in size as the cells that enclose the embryo sac divide and expand. While the potential size of the grain is now determined, there has been little increase in grain weight.

By 4 to 10 days after flowering, the size of the grain has increased considerably. When squashed it appears to contain only water. This is the watery ripe stage (Z71), and the grain is ready to start filling. The developing grain is still green.

Stage 2 Grain fill (Z73–Z89)

Grain fill lasts for 15 to 35 days. During this stage grain weight increases at a constant rate as carbohydrate and protein are deposited into the grain. The grain moves from what is known as milk stage through to dough stage. The exact stage is determined by the amount of solids in the grain 'milk' or the stiffness of the grain 'dough'.

Milk development (Z71–Z77)
At the early milk stage (Z73) the grain is almost grown to its full length and is one-tenth of its final weight. Filling continues, and by the medium milk stage (Z75), 11 to 16 days after flowering, the grain is half grown.

Dough development (Z83–Z87)
During the dough stage the grain is no longer watery but soft and dough-like. Once the grain has reached the early dough stage (Z83) all the structural

elements are laid down in the grain and it is potentially viable. After this point the filling process continues loading carbohydrate and protein.

The soft dough stage (Z85) is about 21 days after flowering. The grain starts to change colour from green to yellow. Maximum grain weight is achieved at Z86, and the grain has a moisture content of 40%. At hard dough (Z87) the grain is golden.

Stage 3 Physiological maturity (Z90)

Finally, the vascular system supplying the grain with water and nutrients is blocked by a waxy substance; the grain stops growing and turns brown. This is physiological maturity (Z90) and occurs at about 700 degree-days. As the grain reaches maturity the tillers die off.

At physiological maturity the peduncle changes to honey-brown or straw-coloured. After this the grain dries down (Z91–Z94) until the moisture content is low enough to be harvested and stored. The grain is harvest ripe at Z92, when it has a moisture content of 12%.

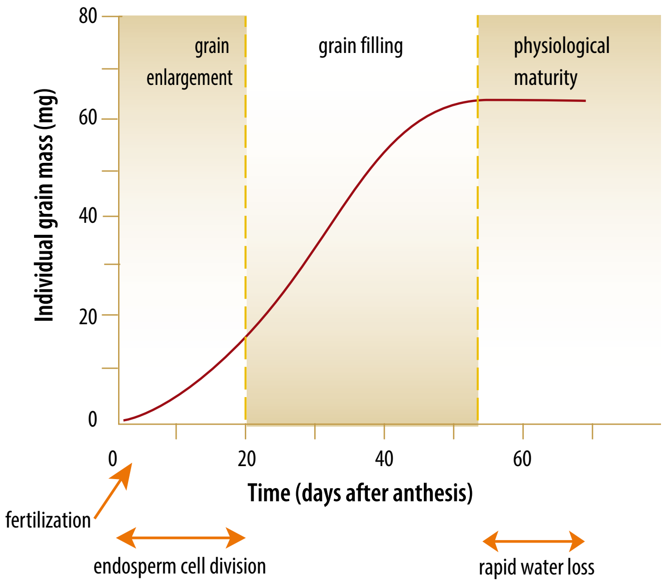


Figure 4–1: Diagramatic representation of the development of a wheat grain. Source: Based on P Stone & M Nicolas, 1996.

- Grain weight increases rapidly during grain filling until physiological maturity is reached.

Sources of carbohydrate

There are two sources of carbohydrate during grain filling. Under favourable conditions, the main source is current photosynthesis from green leaves, in particular the flag leaf. Other plant structures such as the stem, glumes and awns produce some carbohydrate while they are still green.

The other source is reserves stored mainly in the stem, and some in the leaves, from photosynthesis prior to flowering. These are referred to as water-soluble carbohydrates and are particularly important when post-flowering stress occurs (Table 4–1). Stress that reduces photosynthesis during grain filling increases the proportion of carbohydrate that comes from stem reserves. Stresses include moisture stress, heat stress or plant disease. Yield loss from post-flowering stress can be partly offset by translocation of stem reserves.

Although there is some potential for wheat breeders to select genotypes that are more efficient at providing stored water-soluble carbohydrates for grain filling, there is little farmers can do in terms of management to take advantage of this source of carbohydrate.

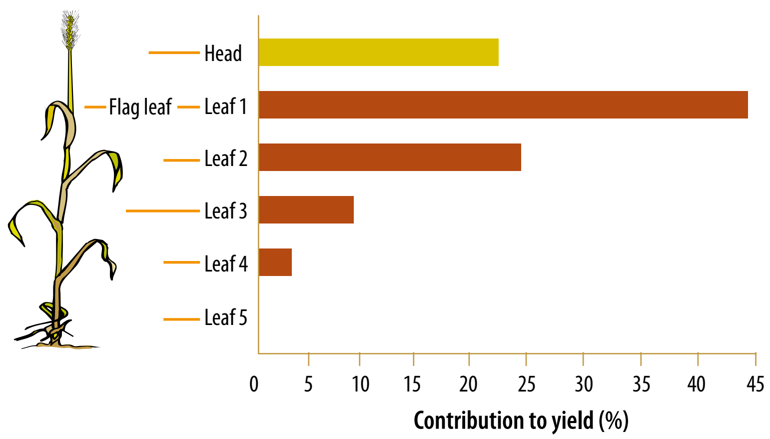
Physiological maturity. Photo: M Dignand.

Sources of protein

Nitrogen stored in the plant is converted into protein for translocation to the grain. Most of the nitrogen that is converted into protein is taken up prior to flowering, stored in the leaves and remobilised during grain fill. The plant can take up nitrogen after flowering, provided the root system is healthy and the soil is moist.

During grain growth, protein is deposited into the endosperm at a rate of 0.15 to 0.20 mg per day.

The nitrogen in the leaves is an important component of chlorophyll and the enzymes involved in photosynthesis. As the nitrogen is remobilised from the leaves to the grain, the leaves stop photosynthesising and die.



- The flag leaf makes the greatest contribution to yield.

Figure 4-2: Photosynthetic contribution of plant parts.
Source: Based on N Fettell, 2006, NSW Department of Primary Industries technical update.

Contribution of plant parts

Different parts of the plant vary in their contribution of carbohydrate to grain fill. The flag leaf makes the highest contribution to photosynthesis (Figure 4–2) because of its relatively large surface area and proximity to the head compared with lower leaves. In high-yielding situations, where canopies are dense, the flag leaf is less shaded than lower leaves.

The high photosynthetic contribution of the flag leaf means it is essential that it remain healthy and protected from disease.

The second, third and fourth leaves make decreasing contributions. Photosynthesis by the head and stem also contribute to grain fill.

Environmental conditions change the contribution of different plant parts. Drought stress lowers the photosynthetic contribution of the flag leaf and other sources, like stem reserves, increase in importance (see Table 4–1). For example, during high temperatures and drought the flag leaf rolls to reduce surface area and decrease water loss, thus decreasing photosynthesis. Some varieties, such as H45, roll their leaves more readily than other varieties.

The contribution of the leaves is also dependent on the length of time the canopy stays green.

Table 4–1: Comparison of the percentage contributions of plant parts to yield under well watered and drought conditions.

	WELL WATERED CONDITIONS	DROUGHT STRESS
Flag leaf	43%	15%
2nd leaf	25%	5%
Head	22%	30%
Pre-flowering stem sugars	10%	50%

Source: N Fettell (pers. comm.).

Measuring protein content

The protein content of the grain is measured as a percentage and is determined by the quantity of protein compared with the quantity of starch. The protein percentage of the grain, usually from 8% to 15%, is important in determining end use. (See *Grain quality and protein* on page 83).

Photo: L Turton.

Factors affecting grain development

In Australia, grain fill occurs as soil moisture decreases and temperatures rise. These environmental conditions affect the rate and duration of grain fill, grain size, and protein content and quality.

Moisture

Adequate soil moisture is essential during grain fill for transpiration and photosynthesis.

Crops with high levels of biomass use a lot of soil moisture and are at increased risk of running out of water during grain fill. This commonly results in pinched or shrivelled grains (screenings). In extreme situations, it leads to haying-off. (See *Canopy management* on page 81).

Moisture stress

Moisture stress reduces the photosynthetic capacity of the crop by causing the premature death of leaves, making less carbohydrate available for transferring to the grain. The rate of storage of carbohydrate in the grain also falls during moisture stress, resulting in a higher percentage of protein.

Table 4–2 shows the impact of moisture stress on yield components, leaf area index and water-use efficiency (WUE) at different growth stages.

Pre-harvest sprouting

Pre-harvest sprouting is when rainfall triggers germination in mature grain still in the head. An enzyme within the grain called alpha amylase begins breaking down starch and protein as part of the germination process. If enough rainfall is received the grain develops a root and shoot, commonly referred to as 'shot and sprung' grain.

The onset of germination and the breakdown of starch and protein reduce grain milling quality. Pre-harvest sprouting also reduces the germination percentage of sowing seed.

Table 4–2: Effects of moisture stress on leaf area index, yield components and water–use efficiency (WUE) of wheat at various stages of growth. ET = evapotranspiration.

PARAMETER		TIMING OF MOISTURE STRESS		
	CONTROL	PRE–ANTHESIS	ANTHESIS	GRAIN FILLING
Leaf area index at booting	5.00	3.30	5.00	5.00
Fertile tillers/m^2	513	658	434	435
Grains/spike	32.7	13	27.1	31.4
1000-grain weight (g)	56.3	55.2	53.7	49.2
Grain yield (g/m^2)	779	559	498	658
Harvest index	0.52	0.50	0.53	0.53
WUE (kg grain/ha mm ET)	16.8	14.6	12.4	15.2

Source: Z Hochman, 1982.

Temperature

Grain development is very sensitive to temperature, which affects:

- grain weight
- the source of carbohydrate
- the quality of the protein.

Heat stress

Heat stress occurs at temperatures above a average daily temperature of 14°C. Yield decreases by 5% for every degree increase in the average daily temperature above 14°C during grain filling. The wheat variety and the timing of heat stress also determine the impact on yield.

A large area of the New South Wales wheat belt has daily temperatures above 14°C during grain filling (see Table 4–3) and experience a corresponding decrease in yield.

Table 4–3: Date at which the average daily temperature reaches 15°C, and daily average temperature at the start and end of the flowering window at different locations in New South Wales.

SITE	DATE AT WHICH AVERAGE DAILY TEMP = 15°C	AVERAGE DAILY TEMP AT START OF FLOWERING WINDOW	AVERAGE DAILY TEMP AT END OF FLOWERING WINDOW
Moree	8 September	14.8°C	16.8°C
Dubbo	27 September	13.6°C	16.6°C
Cowra	17 October	14.5°C	16.6°C
West Wyalong	30 September	13.1°C	16.5°C
Hay	30 September	11.9°C	16.0°C

Source: SILO data 1900 to 2007.

Final grain weight is determined by the rate and duration of grain filling. Both processes are driven by temperature. As the temperature increases above 14°C the rate of grain filling speeds up, while the duration of grain fill shortens, even in well watered crops. The plant speeds up photosynthesis, so that the same amount of carbohydrate is produced despite the reduced duration.

Once temperatures rise above an average daily temperature of 14°C during grain fill, the plant can't increase the rate of photosynthesis sufficiently to compensate for the shorter period of grain fill, so grain weight and yield are reduced. The impact of temperature on the duration of grain fill is represented in Figure 4–3.

The impact of high temperatures on the production of carbohydrate and deposition in the grain reduces grain size and grain yield. Protein deposition in the grain is less affected by heat stress. The result is a higher percentage of protein in the grain. Figure 4–4 demonstrates this concept. As the amount of starch decreases, the percentage of protein increases, even though the actual amount of protein hasn't changed.

- Increase in average temperature from 21°C to 30°C almost halved the duration of grain fill.

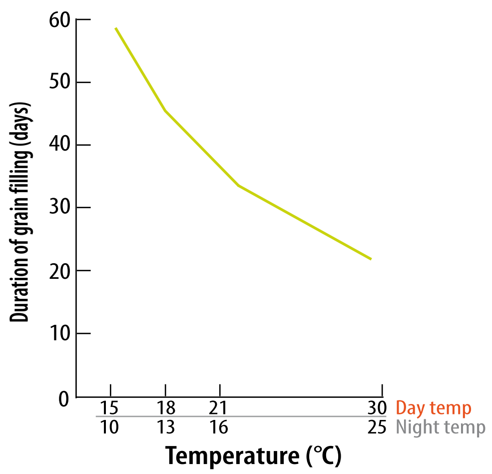


Figure 4–3: Effect of temperature on the duration of grain fill.
Source: Based on Sofield et al., 1977.

Heat shock

Heat shock occurs at temperatures above 35°C and reduces grain size and grain yield by decreasing the rate and duration of grain fill. As an example, a 4-day period of heat shock may cause a 20% loss in yield. Short periods of heat shock during grain fill are common in Australia.

The effects of heat shock are not cumulative, so the maximum temperature determines the extent of the damage, not the length of time the temperature remains over 35°C. Once there has been a heat shock event any subsequent events have less effect on yield than the initial heat shock event. If cool temperatures follow, yield losses can not be reversed.

Crops that are haying-off are likely to experience a greater loss in yield from heat shock, because less water-soluble carbohydrates have been stored for translocation into the grain when photosynthesis slows. (See *Nitrogen* on page 78 for more detail on haying-off).

Some varieties have a higher heat stress tolerance that is thought to be due to membrane stability, increased protein stability and a higher level of heat shock proteins.

Heat shock proteins are manufactured by the plant when cells are 5° to 10°C above their normal growth temperature. They are involved in repairing and protecting structures damaged by heat or other stresses like drought and salinity.

To minimise risk of heat shock, it is critical to time sowing so that flowering and grain filling occur before the high temperatures of early summer.

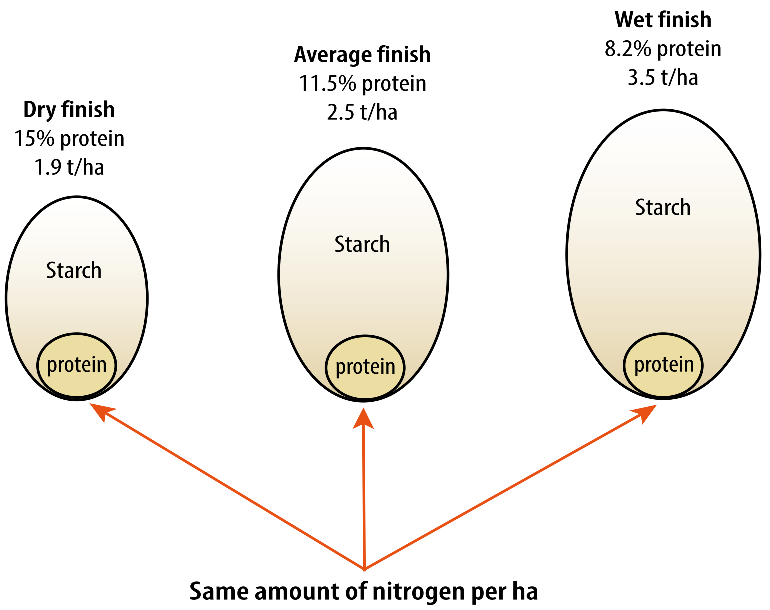


Figure 4–4: Different seasonal finishes affect the ratio of starch and protein in the grain and therefore the percentage of protein.

Nitrogen

Nitrogen is an essential component of protein, and its availability during grain filling is important in determining final yield and quality.

By flowering time, potential yield is set, so nitrogen applied after flowering is converted to amino acids and translocated to the grain as protein, increasing grain protein concentration.

The wheat plant responds differently to nitrogen fertiliser, depending on the amount of nitrogen already available to the plant. If there is very little nitrogen available, a small addition of nitrogen mainly increases grain starch content, and therefore yield.

As the amount of nitrogen increases, it still increases starch but has a greater effect on protein. Once the amount of nitrogen applied is sufficient to maximise yield, further nitrogen no longer increases starch levels but continues to increase the protein content of the grain (see Figure 4–5).

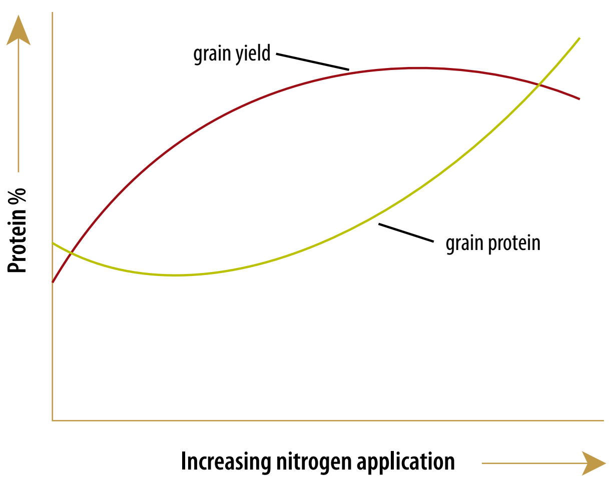
The application of nitrogen is critical to canopy management, especially in terms of the use of water and resources.

Crops with high nitrogen levels have an increased risk of haying-off, producing very high levels of biomass early in the season. The increased biomass draws heavily on the products of photosynthesis, which are used to build the additional tillers and leaves, leaving very little to store as water-soluble carbohydrates for translocation during grain fill. If moisture stress occurs the grain is unable to be filled.

The high level of biomass also uses a lot of water, leaving less for grain fill. Crops that are haying-off have also been shown to extract less water overall.

The timing of nitrogen applications has a significant impact on final yield, as it influences the size of the canopy, the number of tillers produced, and the final number of heads/m². A recent research project carried out on the Liverpool Plains measured the impact of the timing of nitrogen applications on yield, quality, nitrogen and water-use efficiencies, and financial returns. The impact on heads/m² is presented in Figure 4–6.

Overall, the research found that there was a significant increase in grain yield with the application of nitrogen, regardless of timing. However, the increase in yield was highest with 100% application at sowing and split applications at sowing and Z31, and lowest with single application at Z39 (Figure 4–7).



- Once the amount of nitrogen applied is enough for maximum yield, additional nitrogen increases the protein percentage.

Figure 4–5: Relationship between nitrogen application, grain yield and grain protein percentage.
Source: Based on W Anderson & J Garlinge, 2000.

Disease

Disease may reduce both the canopy size and the duration of green leaf, meaning that the crop depends more on stored reserves to complete grain fill. Generally this leads to lower yields and grain weight. Studies show yield decreases of 50%, mainly from lower grain weight, from yellow spot or stem rust.

Some foliar diseases simply reduce the leaf area available for photosynthesis, with a proportional loss in yield. Others cause the plant to produce an enzyme called invertase that traps the products of photosynthesis in the leaves, preventing them from reaching the grain.

Root and crown diseases lower the ability of the plant to take up water, intensifying the impact of moisture stress and decreasing photosynthesis. This usually results in reduced 1000-grain weight.

Disease also causes the plant to divert resources to the disease sites to fight infection, reducing the supply of resources to the grain.

- Final head number increased significantly with the application of nitrogen.
- All nitrogen timings produced larger crop canopies than no nitrogen application.
- Earlier nitrogen applications produced more heads/ m^2.

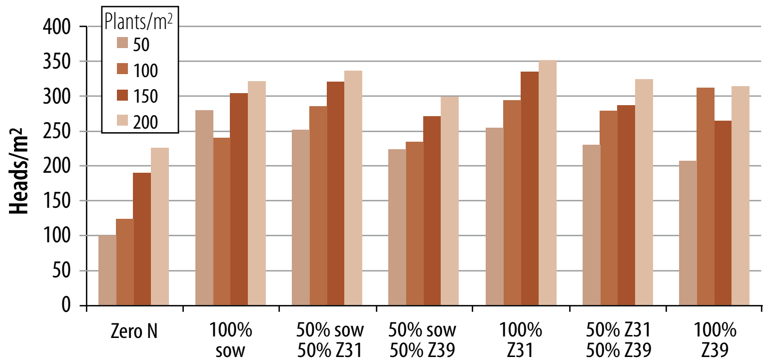


Figure 4–6: Influence of nitrogen timing strategy and plant population on tiller population (heads/m^2) in cv Ventura at Z85, 7 November.
Source: Based on N Poole et al., 2007

- There was a significant decline in yield with the later nitrogen timing compared to the seedbed timing, especially with the single dose application at Z39.
- Yield decrease with later applications was less with split applications of 50% at sowing.

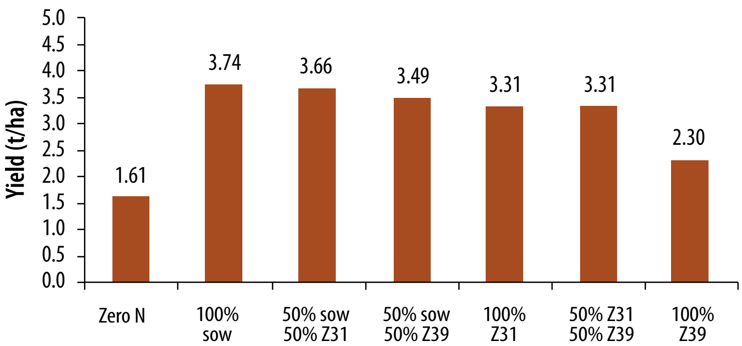


Figure 4–7: Influence of nitrogen timing on grain yield of cv Ventura (mean of all plant populations).
Source: Based on N Poole et al., 2007.

Grazing

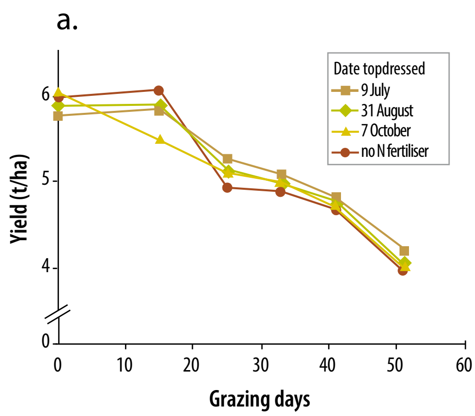
The impact of grazing on yield is highly variable and depends on many factors, including the growth stage when stock is removed, the duration of grazing and the seasonal conditions.

Grazing reduces the leaf area at flowering, thus lowering photosynthesis during grain filling and reducing the storage of reserves. Grazing does not alter the ability of the plant to draw on stored reserves, but it does reduce the amount available. Stored reserves are completely exhausted by maturity in crops that have been grazed. However, because there are fewer stored reserves, photosynthesis during grain filling makes the greatest contribution to final yield and protein percentage.

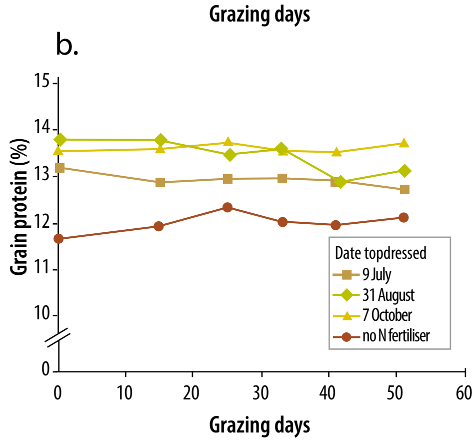
Grazing also delays flowering, which shortens the duration of grain fill, and causes it to occur at higher temperatures and lower moisture.

The duration of grazing is one of the most significant factors in determining the impact on yield. Results of recent research carried out near Holbrook in New South Wales show that as duration increases there is a corresponding decrease in yield (Figure 4–8). The yield components most affected by grazing were grains/head and grains/m^2. Both decreased by 50% to 60% in response to grazing.

The results of this research also showed that the application of nitrogen in grazed crops had no effect on yield, but did increase grain protein.



- Grazing did not significantly affect yield for the first 15 days.
- As the duration increased, the decrease in yield became more significant.
- Nitrogen applications had no effect on yield.



- The duration of grazing did not affect the percentage of protein in the grain.
- Nitrogen application had no effect on yield but did increase grain protein percentage.

Figure 4–8: (a) Yield and (b) grain protein in crops grazed for different durations and managed with different nitrogen (N) fertiliser strategies. Topdressed with 60 kg/ha of N fertiliser on the dates specified. The bars indicate least significant difference.
Source: Based on J Virgona et al., 2006.

Canopy management

The aim of canopy management is to maintain the size and duration of green leaf to maximise photosynthesis during grain fill. The canopy needs to stay green and photosynthesising until the mid-dough stage, when the grain starts to dry down.

Available soil moisture after flowering is a significant factor. It determines whether the number of heads grown during the vegetative period can be filled, as well as the final grain weight.

To maximise yield potential, a balance is needed between the canopy, which is photosynthesising and producing carbohydrate, and the head, which uses carbohydrate and protein to fill its grain. If the canopy becomes too big it competes with the growing heads for resources, especially during the critical 30-day period prior to flowering. This is illustrated in Figure 4–9.

After flowering, temperature and evaporative demand increase rapidly. If there is not enough soil moisture, the canopy dies faster than the grain develops, leading to small, pinched grain. This is more likely with a larger canopy from early sowing or the addition of nitrogen fertiliser.

The extreme of this scenario is 'haying-off', where a large amount of biomass is produced early, using a lot of water and resources. Under moisture stress, there is not enough moisture to keep the canopy photosynthesising, and not enough stored water-soluble carbohydrates to fill the grain.

To attain maximum yield, it is important to achieve a balance between biomass and resources. The inputs that can be managed are:

- plant population
- nitrogen
- sowing date
- diseases and insects
- row spacing
- surface stubble.

Of these inputs, plant population and nitrogen use are the most important to canopy management.

Photo: J Gasparotto.

- High-biomass crops, with pinched grain from lack of moisture during grain fill, lie to the right of the maximum yield line and have a low harvest index.
- Crops that have low biomass and are not able to set enough grain for high yield but have enough moisture for grain fill are on the left of the maximum yield line. These crops have a high harvest index.

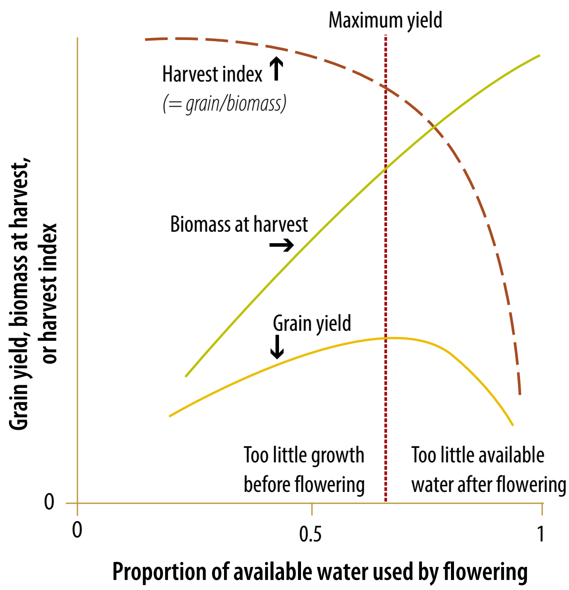


Figure 4–9: The proportion of available water supply used for flowering in dryland crops has a large influence on the yield of the crop, depending on the amount of dry matter at harvest. Source: Based on J Passioura, 2002.

Measuring crop performance

Yield

Yield is determined by four components:

- number of heads/m²
- number of spikelets per head
- number of grains per spikelet
- weight per grain.

The yield components develop sequentially, although there is some overlap, as shown in Figure 4–10. Head and spikelet number are set well before flowering, grain number at around flowering, and grain weight between flowering and maturity. Grain weight is the least variable of the yield components because it is largely determined by genetic potential of the variety. (See *In the paddock: Estimating yield* on page 87).

Number of heads

Head number is the first yield component formed and is set by tiller number/m². Tiller number/m² depends on initial plant population, the variety and environmental conditions (in particular nutrition). In most wheat crops, the plant produces more tillers than survive to produce heads. Stress and competition for nutrients causes tiller death.

Number of spikelets per head

The number of spikelets per head is determined by variety and environmental conditions. Spikelets per head range from 18 to 22 and is determined by variety and environmental conditions. Stress at the time of spikelet development can reduce spikelet number and head size.

Number of grains per spikelet

Grain number per spikelet is determined by the number of fertile florets per spikelet. The central spikelet of a head can initiate up to 10 florets, but in a typical wheat head only three or four of these florets set grain.

When the flag leaf is fully emerged and the boot is visible (Z41–Z45) there is competition for resources between the rapidly growing head, peduncle and the stem. This competition leads to some floret death.

Floret death can also occur when there is a large number of heads/m², which may happen with high seeding rates or large applications of nitrogen. Photosynthesis per shoot is low, reducing the production of resources.

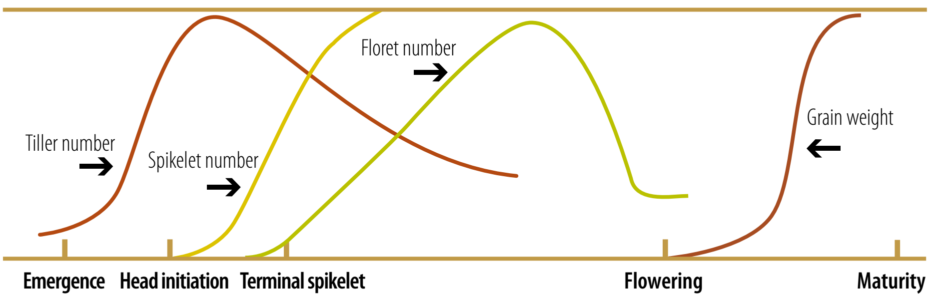


Figure 4–10: Development of yield components .
Source: Based on W Anderson & J Garlinge, 2000.

- Yield components develop in sequence.
- Some components overlap.
- Three of the four components are set by flowering time.

Weight per grain
The weight per grain is commonly expressed as 1000-grain weight. Factors that affect the 1000-grain weight include:

- genotype
- storage capacity of the grain
- photosynthetic capacity of the upper leaves, peduncle and head
- stem reserves
- position within the spikelet
- spikelet position within the head.

Grains from the top and bottom of the head, and the outside of the spikelet are usually smaller than those in the centre. Grains from later formed tillers are also smaller.

Soil moisture, temperature and plant density are the main environmental factors that influence 1000-grain weight.

Yield compensation

The wheat crop can respond to improving or deteriorating conditions almost to maturity. This is largely due to the wheat plant's capacity to compensate for the availability of resources by increasing or decreasing some or all of its yield components.

This ability to compensate means that the plant produces yield even when one or more of the yield components is affected by environmental conditions or management actions. For example, low tiller number caused by stress during tiller formation can be compensated for by a larger number of spikelets per head and/or more grains per spikelet. Another example is that a large numbers of heads/m^2 can be compensated for by smaller heads or lower 1000-grain weight.

Although the plant can adjust according to conditions, maximum yield is most likely when the plant has to do the least amount of compensation.

Grain quality and protein

Grain size and protein percentage are important determinants of grain quality. Grain protein concentration and composition influence the quality of the flour produced from the grain.

The concentration of protein in the grain is dependent on the amount of carbohydrate and protein deposited in the grain.

Most translocation of protein occurs from the lower leaves and is much less affected by high temperature than carbohydrate. As a result, the high temperatures that reduce the depositing of carbohydrate indirectly increase the protein percentage.

The amount and type of protein determine dough properties. Dough properties affect how well bread rises and are determined by variety, temperature during grain fill and protein content of the grain. Heat stress increases the protein concentration and therefore increases dough strength.

Heat shock, on the other hand, changes the type of protein produced, which reduces dough strength. Bread baked with flour that has low dough strength does not rise well.

Harvest index

The harvest index is a method for measuring the proportion of above-ground dry matter that is grain. Early Australian wheat varieties were tall and had a low harvest index because they were mainly being grown for hay production.

The shift towards grain production saw plant breeders place greater importance on grain yield, and the harvest index began to increase. A high harvest index means that there is more grain for each tonne of dry matter. In New South Wales, harvest indexes range from 35% to 40% and vary from season to season. A harvest index of 20% is low and may indicate that problems like haying-off or frost have

occurred. A harvest index of 45% or more indicates good conditions during grain filling. (See *In the paddock: Calculating harvest index* on page 88).

Reducing plant height is the main way plant breeders have increased the harvest index and yield. It reduces the risk of lodging, and more importantly, it leads to a more efficient distribution of resources within the plant. There is less competition between the stem and the head for resources when grain number is being determined.

Water-use efficiency

Water-use efficiency (WUE) is a method of measuring how efficiently crops have used available moisture. It is used to set a target yield based on available soil moisture and expected in-crop rainfall. (See *In the paddock: Calculating WUE* on page 89).

The relationship between water use and yield is demonstrated in Figure 4–11. For each millimetre of water available above 110 mm, grain yield is produced at a maximum rate of 20 kg/ha per millimetre of water. Approximately 110 mm of water must be available to the crop before any yield is obtained. The 110 mm is related to water lost to evaporation and required to grow the crop. The amount of water lost to soil evaporation is higher in areas where in-crop rainfall is more frequent and is less where crops depend more on stored moisture.

There are many assumptions when calculating water-use efficiency. For example, adequate nutrition and weed control are required for crops to use water efficiently. Recent research has found that nitrogen application at sowing or split between sowing and Z31 maximises WUE.

The actual WUE achieved varies from season to season, as the timing of rainfall has a large impact on WUE. Rainfall just before or after flowering is used more efficiently than rain at other growth stages. The size of the fall is also important. One 20-mm fall is likely to have less evaporation than five 4-mm falls over several weeks.

A low WUE may mean that there has been a problem with disease, nutrition or climate that has prevented the crop from reaching its full potential.

Software packages like Wheatman®, APSIM® and Yield Prophet® are now available to do these calculations, taking into account seasonal conditions.

- Yield is linked to water use.
- 110 mm of water must be available to the crop for there to be any yield.
- The sloping line indicates the potential yield from water used by the crop.

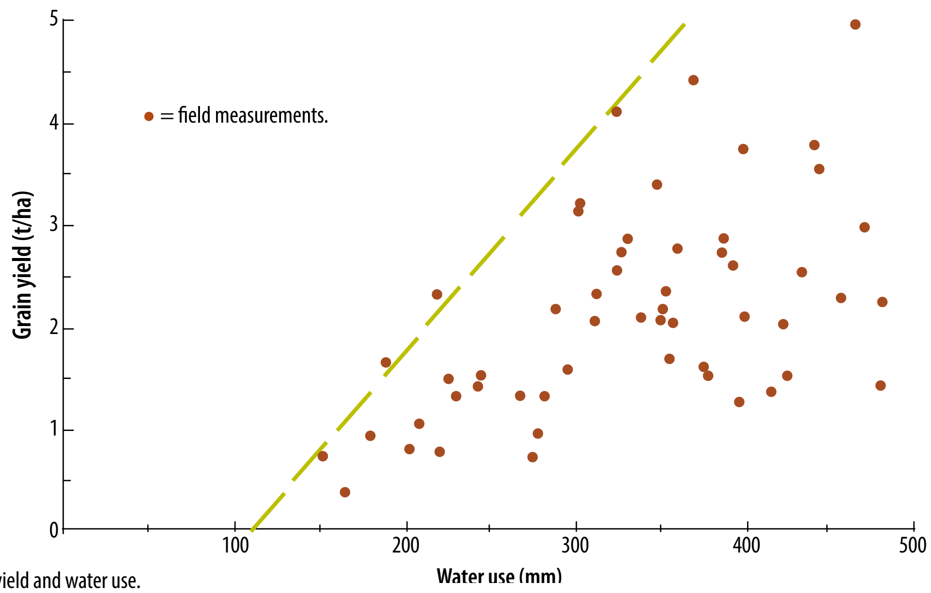


Figure 4–11: The relationship between grain yield and water use.
Source: Based on R French & J Schultz, 1984.

Photo: J Gasparotto.

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IN THE PADDOCK

The following are some examples of what can be done in the paddock to demonstrate the physiology discussed in this section. These are practical exercises to help farmers assess the progress of their crop at this stage.

Estimating yield

Aim: to estimate yield in the paddock.

1. Count the number of heads per 0.5 m row.
2. Do this at 10 locations across the paddock.
3. Add the 10 counts together and divide by 5 to get the average number of heads/m of row.
4. Multiply the head counts by the row spacing factor.

17.5 cm = 5.71	20 cm = 5.00	33 cm = 3.03
22.5 cm = 4.44	25 cm = 4.00	36 cm = 2.77
27.5 cm = 3.36	30 cm = 3.33	40 cm = 2.50

5. Count the grains in at least 10 heads and calculate the average number of grains per head.
6. Count a range of head sizes to get an accurate estimate.
7. Use an estimate of seed weight between 0.030 and 0.045 grams. Seed weights can vary between seasons.

$$\text{Yield (t/ha)} = \frac{\text{heads/m row} \times \text{number of grains/head} \times \text{estimated seed weight (g)}}{100}$$

YIELD (t/ha)				
COUNT	NUMBER OF HEADS/M²	NUMBER OF GRAINS PER HEAD	ESTIMATE OF GRAIN WEIGHT	YIELD (t/ha)
Example	163	5714	0.035 g/grain	2
Example	408	14285	0.035 g/grain	5
Example	571	20000	0.035 g/grain	7
Example	734	25714	0.035 g/grain	9
1				
2				
3				
4				
5				
Average				

IN THE PADDOCK

Assessing grain size variation

Aim: to assess grain size variation in the head.

1. Collect 10 wheat heads from the main stems across a paddock.
2. Using a head from one plant, identify the basal, middle and apical spikelet positions.
3. Also identify the different floret positions on the head.
4. Pull out the grains from the primary florets in each spikelet and put them in one dish.
5. Collect the grains from the outside florets and place then in another dish.
6. Weigh the different dishes to compare the variation in grain size.
7. Repeat the exercise, this time collecting grains from the basal, middle and apical spikelets.
8. The exercise can also be used to compare the grain size difference between the main stem and the later tillers.

Calculating harvest index

Aim: to calculate harvest index using a method described in Farming Ahead and developed by Anthony Van Herwaarden of CSIRO.

1. Cut several small sheafs of wheat at ground level around a paddock and place a couple of rubber bands around each sheaf to hold it together.
2. Measure the height to the top of the average head (excluding awns) and the length of the average head, both in centimetres.
3. Place the sheaf over the edge of a table or other sharp edge and measure the distance from the base of the stems to the point at which the sheaf just balances (X).
4. The harvest index is calculated using the formula:

$$\text{Harvest index} = \frac{(2X - \text{height to the top of the average head})}{(\text{height to the top of the average head} - \text{length of the average head})}$$

IN THE PADDOCK

Calculating WUE

Aim: to use rainfall records to estimate the water-use efficiency (WUE) of a crop.

1. Using your rainfall records, calculate the amount of water that was available to the crop. The formula is:

   Total available water (mm) = 25% fallow rainfall + in-crop rainfall

2. It is assumed that 25% of the rainfall during the fallow will be stored in the soil and available to the crop. This varies depending on stubble cover, weed growth and the rainfall pattern.

3. Subtract 110 mm from the total available water to account for the water required by the crop to grow and for losses from run-off and evaporation. The WUE is calculated using the following formula:

$$\text{WUE (kg/mm/ha)} = \frac{\text{crop yield (kg/ha)}}{\text{total available water (mm)} - 110\text{ mm}}$$

WUE (kg/mm/ha)			
	PADDOCK 1	PADDOCK 2	PADDOCK 3
Fallow rainfall			
In-crop rainfall			
Total water supply			
Yield (t/ha)			
WUE			

Glossary

Aleurone
The outermost cell layer of the endosperm, usually only one cell thick and the only endosperm tissue alive at maturity. The cells of this layer synthesise enzymes needed at germination.

Anther
The terminal part of a stamen, producing pollen, in pollen sacs.

Anthesis
Flowering; the moment when pollen is released from the anthers.

Apex
The tip of an organ.

Apical meristem
Growing point; a zone of cell division at the tip of the stem or root.

Auricles
Small hairy projections that extend from the leaf collar.

Awn
A long spine on the wheat head that projects from the tip or back of the lemma or glumes.

Axil
The angle where the leaf joins the stem.

Bract
A modified leaf, or leaf-like structure.

Brush
A collection of hairs at the distal end of the wheat grain.

Carpel
The female part of the flower. A carpel consists of three parts: the ovary, which becomes the seed after fertilisation; styles, extensions of the ovary; and stigmas, specialised filaments on which the pollen falls and germinates.

Coleoptile
A protective cylindrical sheath-like structure that surrounds the first leaf.

Dormancy
A resting period in the life of a plant when growth slows or appears to stop. In cereals this is between the start of seed dry-down and maturity.

Dorsal
On or near the back; the side of the organ away from the central axis.

Double ridge
Marks the transition from the 'vegetative' to the 'floral' state in the shoot apex. Growth of the leaf ridge stops and the floral ridge begins to grow, giving a 'double ridge' appearance to the shoot apex. The plant no longer produces leaves and develops only flower parts.

Early milk
A description of the grain in early development; when punctured the grain contents are starting to appear milky.

Embryo
Part of the seed that contains the main plant structures. It is made up of the scutellum, plumule and radicle.

Endosperm
A nutritive tissue within the seed that surrounds the embryo and provides energy for germination.

Fertilisation
The union of male and female reproductive cells during the process of sexual reproduction.

Filament
The stalk of a stamen.

Flag leaf
The uppermost leaf on the stem.

Floret
The wheat flower.

Glume
A strong protective bract on the outside of the spikelet, at the base of the wheat head.

Hard dough
A description of the grain at maximum dry weight. The grain is hard to puncture and has started to dry off.

Harvest ripe
The grain has dried off and is ready to be harvested.

Imbibe
Absorb water.

Internode
The part of a plant stem between two nodes.

Leaf collar
The point where the leaf sheath joins the leaf blade, with two features: the ligule and auricles.

Lemma
The lower of two bracts that protect the floret.

Lodicules
Two small structures below the ovary that swell up at flowering, forcing open the enclosing bracts, exposing the stamens and carpel.

Ligule
Thin colourless membrane around the base of the leaf collar.

Medium milk
A description of the half-grown grain. When it is punctured the contents are milky.

Meristem
Growing point where active cell division takes place and permanent tissue is formed.

Node
The part of a plant where one or more leaves grow. The nodes are separated on the stem by the internodes.

Ovule
The part of the plant that, after fertilisation, develops into the seed.

Palea
The upper of two bracts enclosing the floret.

Peduncle
The final internode of the plant stem that bears the flower.

Plumule
Growing point of the seed that develops into the shoot bearing the first true leaves.

Pollen
The male gametes, which are produced in the stamens.

Pollination
The transfer of pollen from an anther (the male reproductive organ) to a stigma (the receptive part of the female reproductive organ).

Primordia
Organs in their earliest stage of development.

Rachilla
The axis in the centre of a spikelet; the secondary axis of the head.

Rachis
The primary axis of the wheat head; it bears the spikelets.

Radicle
The part of a plant embryo that develops into the primary root.

Scutellum
A shield-shaped structure in the seed; it absorbs the soluble sugars from the breakdown of starch in the endosperm.

Shoot apex
See apical meristem.

Soft dough
Grain at maximum fresh weight. When the grain is punctured the contents are still wet but starting to become floury.

Spikelet
Part of the head consisting of several florets on a thin axis, the rachilla.

Stamen
The structure in a flower that produces pollen grains, consisting of a stalk (filament) and an anther.

Stigma
The glandular sticky surface at the tip of the carpel of a flower; it receives the pollen.

Terminal spikelet
The last spikelet produced, marking the completion of the spikelet initiation phase. It is at right angles to the other spikelets.

Tiller
A lateral shoot that develops from the axillary bud of leaves at the base of the stem.

Water ripe
A newly pollinated grain. When the grain is punctured the contents are very watery.

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